BI-DIMENSIONAL FEEDING ECOLOGIES AND FOOD WEB STRUCTURE: A CONCEPTUAL FRAMEWORK LINKING TROPHIC AND SPATIAL PROCESSES IN AQUATIC ECOSYSTEMS, WITH APPLICATION TO MERCURY BIOACCUMULATION IN FISH

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by

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THESIS ABSTRACT

This thesis presents the results of a study of the ecology of fish communities of lakes and reservoirs in Labrador, Canada. The first objective of the thesis was to evaluate the relevance and implications of a bi-dimensional framework to integrate spatially-explicit energy flows in consumer feeding ecology and food web structure. Second objective was to assess whether spatially-explicit bi-dimensional feeding ecologies and food web structures can improve the assessment of mercury (Hg) bioaccumulation in fish. A bi-dimensional framework consists in the integration of horizontal (spatially-explicit) and vertical (trophic) energy flows. This approach is demonstrated in comparative studies of fish populations and communities from four pristine lakes. Horizontal energy flows here distinguished between littoral and pelagic carbon contributions to fish consumers in lakes, quantified by variations in stable isotope ratios of carbon in fish tissue. Vertical energy flows described variations in fish trophic position quantified by variations in stable isotope ratios of nitrogen. Comparing life-stage and among-lake patterns of trophic position and littoral-pelagic resource use in four fish species demonstrated that bi-dimensional feeding strategies are determined by species ontogeny and ecosystem characteristics. Comparisons of lake-specific bi-dimensional food web structures estimated from community averages of fish trophic position and littoral-pelagic foraging demonstrated that spatially-explicit community organization is related to consumer species composition, to primary productivity constraints and to physical ecosystem structure. Applied to the understanding of Hg bioaccumulation, a bi-dimensional framework integrated spatial influences on Hg exposure and trophic transfers in aquatic ecosystems and improved predictions of fish Hg concentrations. Horizontal energy flows in this case further distinguished between allochthonous-autochthonous carbon contributions to primary producer-consumer. A bi-dimensional approach revealed that aquatic ecosystems with longer food chains, greater assimilation of autochthonous carbon at lower trophic levels and greater reliance on littoral carbon by fish, reach greater Hg contamination. The influence of littoral-pelagic resource use on fish Hg levels varied with the type and size of prey consumed across habitat boundaries. Autecological types

distinguish consumers bi-dimensional feeding ecologies as shaped mainly by ontogeny (Quis type), by ecosystem features (Ubi type) or both (Aequivocus type). This classification provided species-specific distinctions for the importance of biological and environmental determinants of Hg bioaccumulation in fish. A bi-dimensional framework provides a solid conceptual basis for spatially-explicit ecological understanding that can improve the assessment of environmental issues.

Keywords: spatial influences, feeding ecology, food web structure, stable isotopes, fish consumers, boreal lakes, reservoir, mercury bioaccumulation, littoral-pelagic habitats, carbon source, trophic position, ontogeny, autecological types.

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This project was offered to me by Dr. M. Robin Anderson, co-supervisor of this thesis. Thank you Robin for the opportunity, for your guidance, but mostly also for the freedom and trust you have provided me with over the past 6 years. Looking back, I think that trust is probably the best thing a supervisor can offer to graduate students, allowing them to follow their intuitions and inspirations. Many thanks also to Dr. Dolors Planas, also co-supervisor of this thesis, and without whom none of this would have been possible. Thank you Dolors for being who you are, for your important help and advise regarding my field work, and for providing the human dimension and support I needed to conduct this research. Special thanks to Moire Wadleigh, who introduced me to the world of stable isotopes with a smile, and to her friend, Frederic Longstaff, who provided guidance, support, and comfort during transition times. I thank Ali Aksu for convincing me that a biologist can do a doctoral degree within the Earth Sciences Department, and Paul Sylvester for allowing me to do so. Thank you Paul for helping with all administrative matters whenever necessary.

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ciel et les journées ensoleillées de cette recherche au cours des dernières années, et qui l'on fait dans la compréhension, le respect, et l'amour. Vous m'avez donné l'espoir et le courage du point final. Merci a petite Isleï qui m'a accompagné dans le dernier print vers la ligne d'arrivée. Merci à toute ma famille qui m'encourage et me supporte même sans parfois comprendre la nature de mes projets. Merci à mes amis, et plus particulièrement aux amis de St-John's qui m'ont hébergée dans l'amitié ces dernières années : Dounia et Thomas, Pia et Alejandro, Delf. Merci de votre générosité, merci pour tous les moments passés en votre compagnie qui me sont si chers. Merci spécial à toi Pia qui t'es souvent trouvée sur ma route dans des moments difficiles et qui m'a beaucoup donné. À vous ainsi qu'à beaucoup d'autres, famille et amis, Maman, Papa, Linda, Tara, Monyse, Jean-François, Françoise, André, Cathia, Cathy, Martine, Étienne, Marie, Éric, Marie-Marthe, Sylvia, Marie-Hélène, Stéfanie, Stephen, Agathe, Andry, Sara, Suzanne, Steve, Ashley, et plein d'autres encore, un vent d'amour et de remerciement. Vous faites partie de ce que je suis et de ce que je fais.

Enfin, merci à Christian Bobin de nous rappeler l'essentiel qu'on oublie trop souvent:

« L'intelligence n'est pas affaire de diplômes. Elle peut aller avec mais ce n'est pas son élément premier. L'intelligence est la force, solitaire, d'extraire du chaos de sa propre vie la poignée de lumière suffisante pour éclairer un peu plus loin que soi –

vers l'autre là-bas, comme nous égaré dans le noir »

- Bobin, C. (1994)

Ainsi, je dédie cette thèse à l'intelligence de tous ceux que j'aime.

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CHAPTER 4

LIST OF ABBREVIATIONS AND SYMBOLS

Ashua	Ashuapamatikuan Lake
Atik	Atikonak Lake
Biomass(peri)	periphyton Biomass
BT	Brook Trout
Chla	Chlorophyll-a
Chla(pel)	pelagic Chlorophyll-a concentration
Chla(peri)	periphyton Chlorophyll-a concentration
%Chla(peri)	periphyton percent Chlorophyll a
$\%C_{LITT/PEL}$	percent reliance on littoral versus pelagic carbon sources estimated from stable carbon isotopes
ComComp	community composition
Darea	lake drainage area
$\delta^{13}C$	stable carbon isotope ratio
$\delta^{15}N$	stable nitrogen isotope ratio
DRatio	drainage ratio (ratio of lake drainage area over lake surface area)
Enaka	Enakapeshakamau Lake
FL	fork length
Hg	mercury
$[Hg]_{(aq)}$	aqueous mercury concentration
$[Hg]_{(peri)}$	periphyton mercury concentration
$[Hg]_{(SPM)}$	suspended particulate mercury concentration
LArea	lake surface area

LNS	Long Nose Sucker
LT	Lake Trout
Lperi	lake perimeter
Mista	Mistashini Lake
NP	Northern pike
Papaua	Papauakamau Lake
PAratio	ratio of lake perimeter over lake area
sc	size class
SE	standard error
SD	standard deviation
SDI	shoreline development index
%SexI	percent sexually immature individuals
SPM	suspended particulate matter
TrophP	trophic position estimated by stable nitrogen isotope
WF	White Fish
WS	White Sucker
Zmax	maximum depth

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INTRODUCTION AND OVERVIEW

Food web structure describes feeding relationships and interactions among organisms within an ecosystem. It is a leading concept in ecology that relates trophic patterns with the dynamic processes that modulate them (Pimm 1982). Food web structure determines the flow of energy, nutrients and contaminants through ecosystems (Hebert et al. 2006). Understanding food web structure and the ecological processes underlying community organization, may thus improve our comprehension of anthropogenic impacts on natural systems and facilitate the evaluation of Hg bioaccumulation in aquatic environments.

1. INTEGRATING SPATIAL CONSIDERATIONS IN ECOLOGICAL STUDIES

1.1. RECENT EVIDENCE FOR THE IMPORTANCE OF SPATIAL PROCESSES IN AQUATIC FOOD WEBS

Traditionally, food web structure describes vertical trophic positions, trophic transfers and interactions and food chain length in ecosystems. In recent years, horizontal habitat-specific carbon sources and fluxes have emerged as key processes for aquatic food webs (Hecky and Hesslein 1995, Schindler and Scheurell 2002, Vadeboncoeur et al. 2002, Karlsson and Byström 2005, Vander Zanden et al. 2006). Within-lake habitat boundaries allow spatially distinct (i.e. littoral-benthic versus pelagic) and often asynchronous primary producer-consumer population dynamics to occur. These constitute distinct carbon sources-fluxes that can be merged by cross-habitat foraging in mobile secondary and tertiary consumers such as fish. Cross-habitat foraging decouples consumer success from local constraints of productivity and prey dynamics (Polis et al. 1997, Schindler and Scheuerell 2002), affecting trophic interactions, direction of energy flows (trophic

cascades) and stability of food webs (Schindler et al. 1996, Post et al. 2000a, Vadeboncoeur et al. 2005).

1.2. Species and ecosystem determinants of trophic and spatially-explicit resource utilization in consumers

The coupling of spatially distinct or habitat-specific carbon sources by consumers is influenced by spatial patterns in ecosystem structure and consumer life-history strategies (Polis et al. 1997, Schindler and Scheuerell 2002). Ontogeny or life-history strategies are combinations of growth-related traits outlining how species exploit resources and utilize habitat. Ontogeny affects the trophic role of consumers (or "who eats whom" on community-scale), determines life-stage patterns of habitat use in some species (or "who eats where") and establishes the extent to which spatially-explicit resource exploitation is shaped by ecosystems characteristics (Roux et al. 2008). Physical ecosystem structure determines habitat and resource heterogeneity. This affects consumer resource use and community organization directly by determining habitat productivity and availability, or indirectly by shaping community interactions and population dynamics (Fig. I-1). Heterogeneity increases the "effective dimensionality" of population dynamics (Holt 2002) and facilitates otherwise unstable community interactions (Spencer and Warren 1996). Structurally complex habitats provide heterogeneous resource and risk settings (like the presence of refuges) that favour the aggregation of aquatic consumer communities and community interactions (Scheuerell and Schindler 2004, Sass et al. 2006). Refuges for prey and for vulnerable size classes of predators influence both predator and prey recruitment and population size and mediate size-structured predator-prey interactions and density-dependent competition. Structural complexity can also

lower consumer foraging success (Diehl 1988, Sass et al. 2006) while increase foraging opportunities and yields (Whitehead and Walde 1992, Sass et al. 2006).

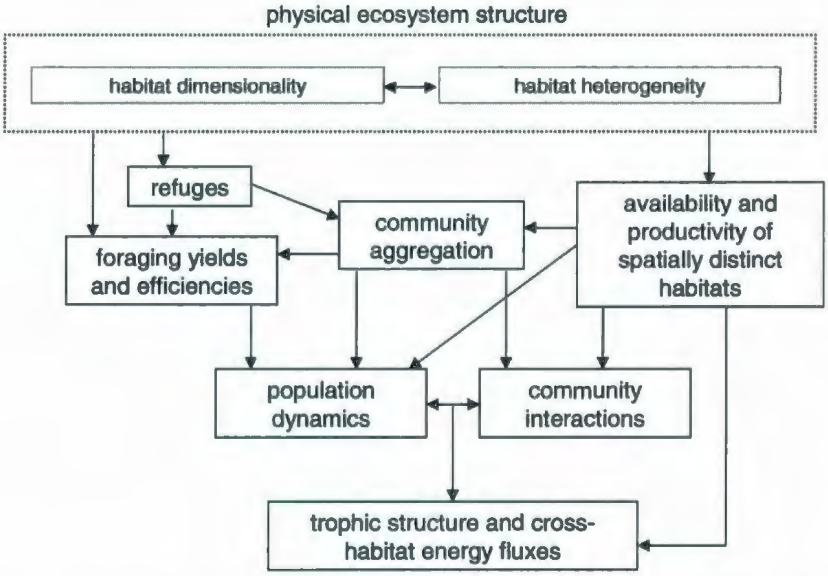

Fig. I-1. Direct and indirect influences of physical ecosystem structure on vertical (trophic) and spatial (cross-habitat) energy flows in aquatic consumers and consumer communities (from Roux et al. 2008).

Thus, depending on species ontogeny, ecosystem characteristics affect habitat coupling by consumers and influence community structure and interactions by determining the heterogeneous character of spatially distinct habitats and habitats boundaries and the size and availability of spatially distinct carbon pools at the base of food webs.

1.3. FROM "WHO EATS WHOM" AND "WHO EATS WHERE" TO "WHO EATS WHOM AND WHERE".

Species traits and ecosystem features determine trophic and spatially-explicit energy flows for consumers in aquatic ecosystems. The importance of spatial processes such as cross-habitat foraging by consumers is increasingly recognized in ecological studies

(Turner 1989, Polis et al. 1997, Tilman and Kareiva 1997, Huxel and McCann 1998, Polis et al. 2004, Lovett et al. 2005). Still, food web ecology lacks a conceptual framework to integrate spatial considerations with traditionally vertical trophic understanding of feeding relationships in biological communities. This doctoral research will argue that both trophic (who eats whom) and spatial (who eats where) processes need to be recognized as the complementary basis for food web structure. Food web structure then becomes a dynamic framework describing "who eats whom and where" in spatially structured ecosystems supported by more than one carbon source. Such understanding provides a conceptual framework that may be suitable to address spatial influences across consumer communities and ecosystem types, and serve to facilitate the evaluation of inter-system variations in fish Hg concentrations among aquatic ecosystems.

2. THE MERCURY PROBLEM

Mercury (Hg) contamination is a complex and widespread environmental problem. In boreal aquatic ecosystems remote from human activities and point sources of Hg emissions, Hg concentrations in fish commonly exceed the advisory limit of 0.5ppm for safe human consumption in piscivorous species (Lindqvist et al. 1991, Bodaly et al. 1993, Schetagne et al. 1999, Kamman et al. 2005).

2.1. SOURCES OF MERCURY TO BOREAL ENVIRONMENTS

Hg is an important and highly variable natural constituent of bedrock, superficial sediments and vegetation (Rasmussen 1994). Atmospheric processes play a prominent role in mobilizing and distributing Hg at the earth's surface (Fitzgerald et al. 1998). Airborne Hg of natural origin released from volcanic emissions, forest fires, or from

degassing of Hg mineral deposits (Wang et al. 2004), has been accumulating in the organic layers of terrestrial soils in boreal environments, ever since the beginning of soil formation after the last glaciation (Schetagne et al 1999). Over the past century, airborne Hg of anthropogenic origin released from solid waste incineration, coal and oil combustion, pyrometallurgical processes, or production of Hg and gold (Wang et al. 2004), has added to the Hg burden of soils and lake sediments across the boreal forest (Schetagne et al. 1999). Anthropogenic Hg emissions to the atmosphere constitute a significant interference in the modern Hg cycle, as evidenced by historical records of Hg deposition preserved in lake sediments and peat bogs (Fitzgerald et al. 1998). Together, coal combustion and solid waste incineration account for more than half of total global Hg emissions (Pirrone et. al. 1996, Wang et al. 2004). Thus it is now recognized that elevated Hg levels in fish from pristine boreal aquatic ecosystems are mainly attributable to long-range atmospheric transport and deposition of anthropogenic Hg sources (Lindqvist et al. 1991, Jackson 1997, Fitzgerald et al. 1998, Wang et al. 2004).

2.2. BIOGEOCHEMICAL PATHWAYS FOR MERCURY IN AQUATIC ECOSYSTEMS

Airborne inorganic Hg is transported and deposited as elemental Hg^0 vapor and divalent (free or particulate-bound) Hg^{2+} (Downs et al. 1998). Hg inputs to aquatic ecosystems can be direct (wet and dry atmospheric deposition) or indirect (surface runoff of catchment deposited Hg) (Fig.I-2). Aquatic environments promote biotic and abiotic methylation processes increasing the bioavailability and toxicity of Hg (Kamman et al. 2005). Together, watershed, littoral, sediment, and water column biogeochemistry determine Hg speciation and bioavailability in aquatic ecosystems (Fig. I-2).

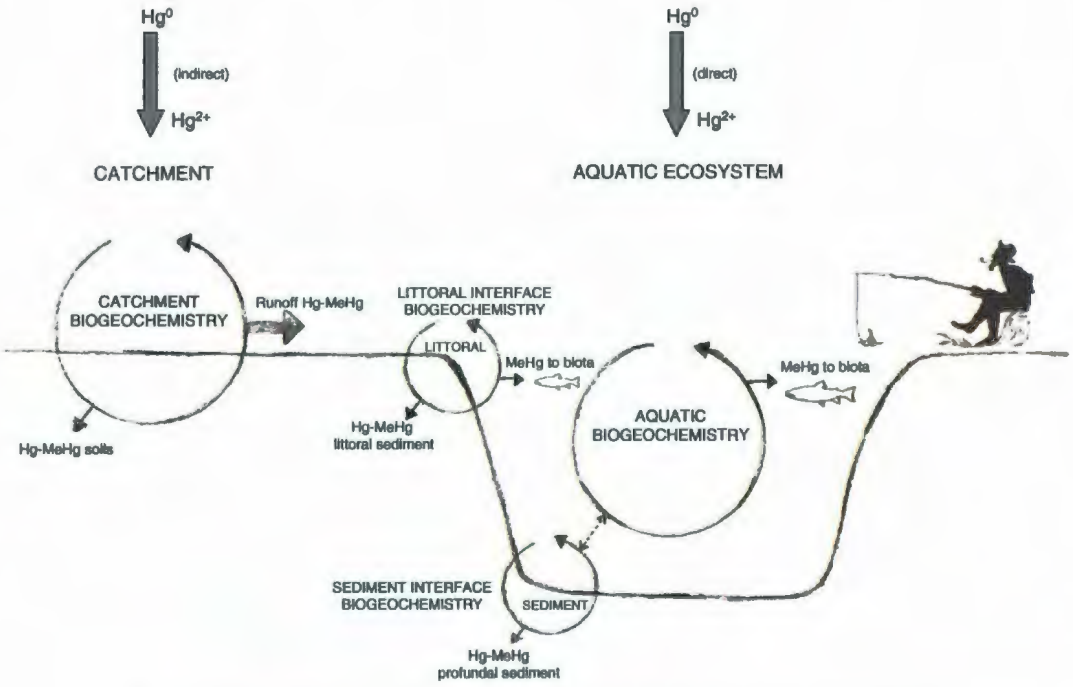

Fig. I-2. Biogeochemical pathways for mercury in boreal aquatic ecosystems.

Toxic methylmercury (MeHg) readily bioaccumulates in aquatic biota and is biomagnified up aquatic food webs to concentrations commonly exceeding those of ambient water by factors of 10^6 to 10^7 in fish consumers (Wiener et al. 2003, Burgess 2005). Contaminated fish in turn convey MeHg burdens to terrestrial food webs via piscivorous birds and mammals. Fish consumption is also the primary route of MeHg exposure in human populations. Thus aquatic ecosystems function as vectors of Hg contamination in the environment.

2.3. EVALUATING THE EXTENT OF MERCURY BIOACCUMULATION IN FISH

Despite an impressive number of Hg-related investigations, Hg pollution management remains complicated by spatial variations in ecosystem response to Hg loadings (Lindqvist et al. 1991, Wiener et al. 2003). This leads to variable Hg accumulation patterns and heterogeneous Hg levels in fish among ecosystems receiving comparable Hg inputs (Lindqvist et al. 1991, Schetagne et al. 1999, Indian and Northern Affairs 2003, Kamman et al. 2005). Several factors have been proposed to account for the observed inter-system and inter- and intra-specific variations in Hg levels in freshwater fish. These include species-specific biological factors and ecosystem-specific factors relating to biological, chemical and physical ecosystem structure. Species-specific biological factors comprise intra- and inter-specific variations in fish body size and age (Indian and Northern Affairs 2003, Wiener et al. 2003, Evans et al. 2005), growth rates (MacCrimmon et al. 1983, Verta 1990, Stafford and Haines 2001, Simoneau et al. 2005), body condition (Greenfield et al. 2001) and trophic position (Kidd et al. 1995, Jarman et al. 1996, Bowles et al. 2001, Bank et al. 2007). Ecosystem factors include (i) determinants of Hg and MeHg inputs to aquatic ecosystems from surrounding watersheds (i.e. wetland cover, watershed slope, catchment disturbance and catchment soil type, organic content and permeability (St-Louis et al. 1994, Garcia and Carignan 2000, Shanley et al. 2005, Desrosiers et al. 2006a), (ii) factors affecting within-lake methylation processes and Hg bioavailability at the base of food webs (i.e. pH, redox conditions, organic and inorganic ligands concentrations, ecosystem size and water temperature (Bodaly et al. 1993, Watras et al. 1998, Sjöblom et al. 2000, Ullrich et al. 2001, Wiener et al. 2003, Chen et al. 2005)) and (iii) biological features determining Hg availability for consumers (primary productivity and food chain length (Lindqvist et al. 1991, Meili

1991, Cabana and Rasmussen 1994, Cabana et al. 1994, Atwell et al. 1998, Kidd et al. 1999)). While numerous studies have identified these factors and their effects on Hg biogeochemical pathways, species and ecosystem determinants of Hg bioaccumulation in fish remain, for the most part, unconnected – and at best valid only for localized areas. Knowledge of common effects and implications for both environmental (system-specific) and biological (species-specific) determinants of Hg levels in fish is still lacking. This continues to impede our ability to predict Hg concentrations in fish, and thus human exposure, even on a regional basis.

3. Food web structure, stable isotopes and Hg bioaccumulation.

Dietary exposure is the main pathway for Hg to fish (Hall et al. 1997). Nearly all (≈99%) Hg in fish muscle tissue is in the form of MeHg (Bloom 1992). Once ingested by aquatic organisms, Hg is bioaccumulated and biomagnified up aquatic food webs, so that top level predators contain significantly more Hg than do fish feeding at lower trophic levels (Fig. I-3). Food web structure defining feeding relationships and interactions among organisms in ecosystems, is thus directly related to Hg movement in aquatic biota, and has been shown to determine Hg levels in fish (Cabana et al. 1994, Cabana and Rasmussen 1994). Stable isotope ratios of carbon and nitrogen provide temporally-integrated information about feeding relationships and energy flows in ecological communities, allowing quantitative representations of all energy pathways leading to an organism (Kling 1992, Vander Zanden and Rasmussen 1999, Post 2002a, Layman et al. 2007); (see Appendix 1 for detail). Due to biomagnification effects, vertical trophic

positions estimated using stable isotope ratios of nitrogen ($\delta^{15}N$), are positively related to Hg concentrations in fish (Kidd et al. 1995, Jarman et al. 1996, Atwell et al. 1998, Kidd et al. 1999, Bowles et al. 2001, Evans et al. 2005).

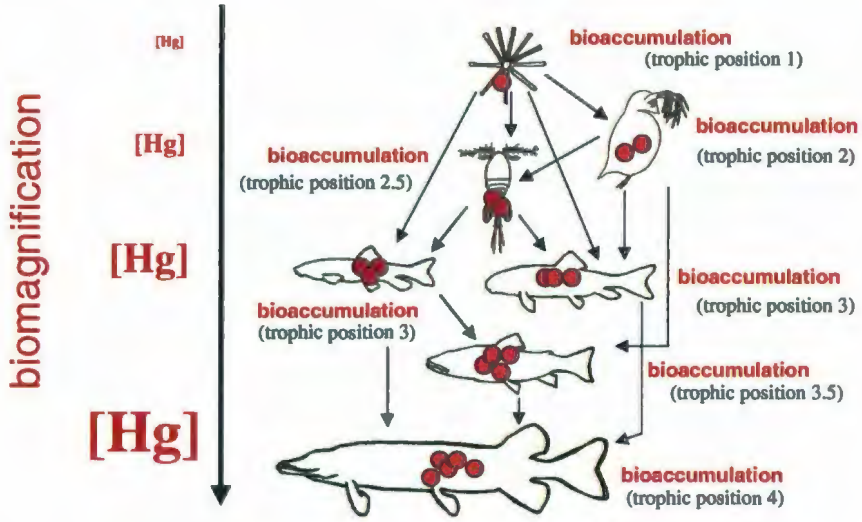

Fig. I-3. Simplified aquatic food web showing Hg bioaccumulation in aquatic organisms and Hg biomagnification with increasing trophic positions (from primary producers at the food web base (trophic position 1) to top predatory fish consumers (trophic position 4)).

Differences in trophic positions and feeding behaviour are useful to explain inter- and intra-specific variations in fish Hg concentrations (Braune et al. 1999, Greenfield et al. 2001, Indian and Northern Affairs 2003). Inter-system variations in the extent of vertical energy flows or food chain length quantified by $\delta^{15}N$, may also account for some of the variation in fish Hg concentrations between similar systems (Cabana and Rasmussen 1994, Kidd et al. 1995). Yet on a regional basis, important variations in fish Hg levels over a relatively narrow range of fish $\delta^{15}N$ values (or large variations in trophic feeding

as $\delta^{15}N$ over a small range of Hg concentrations) have been observed (Evans et al. 2005). This indicates that feeding patterns between trophic levels alone, cannot explain spatial variations in Hg bioaccumulation between fish communities.

More recently however, the use of stable isotopes of carbon ($\delta^{13}C$) to distinguish between different carbon sources-pathways in food webs, has been used to demonstrate an effect of cross-habitat foraging on Hg accumulation in fish (Power et al. 2002a, Gorski et al. 2003, Bank et al. 2007). This suggests some spatial distinction in the regulation of Hg levels between spatially-distinct habitats (i.e. littoral-benthic versus pelagic habitats) in aquatic ecosystems. Recent evidence for Hg methylation and transfer to aquatic biota via littoral periphyton communities (Cleckner et al. 1999, Desrosiers et al. 2006a, Desrosiers et al. 2006b) support this contention. Together, consideration of carbon source (as $\delta^{13}C$) and trophic position (as $\delta^{15}N$) better described Hg accumulation in a sub-Arctic lake fish community (Power et al. 2002a). Thus spatially-explicit resource utilization between habitat boundaries, together with vertical trophic positions, affect Hg bioaccumulation in fish. Moreover, since trophic and cross-habitat energy flows affecting Hg pathways for fish consumers are determined by species traits and ecosystem features, spatially-explicit feeding patterns may provide a link between species and ecosystem determinants of Hg bioaccumulation that should facilitate the evaluation of inter-system variations in fish Hg concentrations.

4. Spatially-explicit feeding strategies and food web structure applied to Hg bioaccumulation.

This thesis research aims to (i) integrate spatial patterns and processes in the definition of consumer-level feeding patterns and community-scale food web structure, and (ii) assess the use of spatially-explicit feeding strategies and food web structure to integrate species and ecosystem determinants of Hg bioaccumulation in fish and facilitate the evaluation of Hg contamination among natural aquatic ecosystems.

These objectives are reached and articulated in two movements, each consisting of two chapters. The first movement expands on a bi-dimensional ecological approach permitting the integration of spatial considerations in food web ecology. This approach is developed and demonstrated in comparative studies of fish populations from natural lakes, in which stable isotope ratios of carbon and nitrogen are used to quantify spatially-explicit feeding patterns in fish consumers (chapter 1) and to extrapolate spatially-explicit food web structure in lake ecosystems (chapter 2). The second movement applies spatially-explicit ecological understanding and theory from the first movement, to the understanding of Hg bioaccumulation in fish on species-specific basis (chapter 3) and across boreal aquatic ecosystems serving subsistence fishing purposes for the Labrador Innu (chapter 4).

5. AN ECOSYSTEM-APPROACH TO HG CONTAMINATION IN LABRADOR

The present research was undertaken as part of the Lakes of the Boreal Forest Ecosystem study within the Collaborative Mercury Research Network (COMERN). COMERN was a pan-Canadian research network established in 2001 (through the financial support of the Natural Sciences and Engineering Research Council of Canada) with the five-year

mission to integrate research efforts in order to reach a better understanding of Hg pathways in Canadian ecosystems. The Lakes of the Boreal Forest Ecosystem study applied an ecosystem approach to the study of mercury in boreal environments, reaching from lakes and their extended drainage areas, to the health of human communities living in boreal environments and consuming fish from boreal aquatic ecosystems. In Labrador, community involvement was an integral part of our research. The project was undertaken in collaboration with the Innu community from Sheshatshui. This community continues to rely to a large extent on subsistence fishing activities and harvests. Traditionally, subsistence fishing is practiced in natural lakes and in the Churchill Falls Reservoir for freshwater fish species, and in Lake Melville for sea-run salmon (Fig. I-4). Concerns related to Hg exposure as linked to the consumption of freshwater fish species with documented elevated Hg levels (Bruce 1979, Scruton 1984, Anderson et al. 1995, Environnment Canada 2004) were thus genuine in the Sheshatshui community. In consequence, our research project involved two principal axes and working teams: (i) the biogeochemical team assessing Hg pathways in all compartments of aquatic ecosystems, and (ii) the human health team evaluating dietary patterns of fish consumption and related Hg exposure in community members. Together, the two teams aimed to link human exposure to Hg through fish consumption with the physical and social context of their environment. For the biogeochemical team of which the present research was part, sampling sites selection and field sampling were actively conducted in partnership with Innu co-researchers. Biogeochemical research aimed to provide a better understanding of Hg behaviour in boreal ecosystems, in order to improve Hg management strategies and policies to reduce human exposure. This was done by relating the amount of Hg in fish to

the biological, chemical and physical properties of aquatic ecosystems and their watersheds.

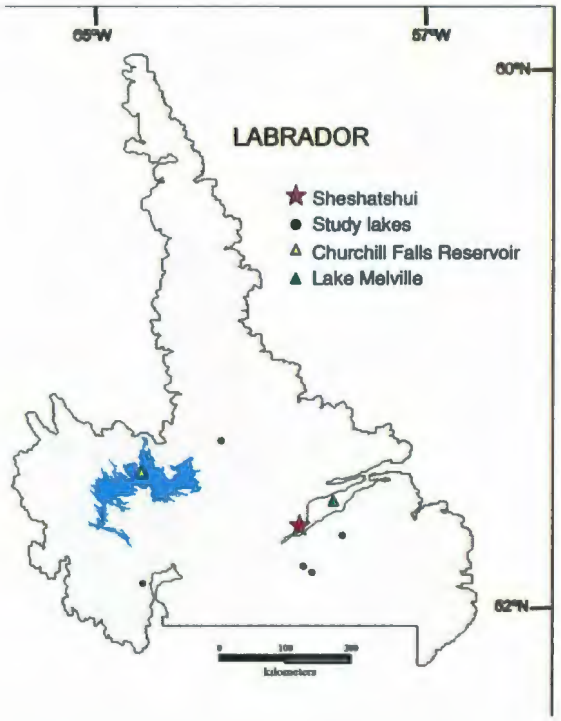

Fig. I-4. Map of Labrador showing the emplacement of the Sheshatshui Innu community and traditional subsistence fishing sites considered for analysis as part of COMERN's Lakes of the Boreal Forest Ecosystem Study.

Collaboration and interactions between biogeochemical and human health researchers were encouraged via annual meetings permitting contacts and exchanges between scientists and graduate students involved in the project. In February 2007, biogeochemical and human health teams joined together for a community workshop in Sheshatshui, where general results that had emerged from collaborative Labrador investigations were presented and given back to the community.

CO-AUTHORSHIP STATEMENT

(i) DESIGN AND IDENTIFICATION OF THE RESEARCH PROPOSAL

Marie-Julie Roux identified and designed every step of her research proposal. Dr. M. Robin Anderson provided Marie-Julie Roux with the opportunity to work on a food web ecology research project related to mercury bioaccumulation in Labrador aquatic ecosystems, and suggested the use of stable isotope techniques as a main approach. Dr. Moire Wadleigh provided Marie-Julie Roux with introductory guidance and assistance with respect to the use of stable isotopes in ecology. Marie-Julie Roux is the sole author of her research proposal.

(ii) PRACTICAL ASPECTS OF THE RESEARCH

Marie-Julie Roux was responsible for organizing and taking part in Labrador field work campaigns and sample collection during summers of 2003 and 2004. Dr. Dolors Planas provided Marie-Julie Roux with field work training and guidance for certain sample type collection and analysis. Marie-Julie Roux was responsible for gathering physico-chemical and water quality information on all study sites, and for all biological sampling and sample preparation for stable isotopes and Hg analysis.

Marie-Julie Roux developed the novel bi-dimensional foodweb approach to incorporate spatial considerations into trophic ecology of aquatic ecosystems. She then demonstrated the utility of this approach by applying it to the explanation of patterns of mercury accumulation in fish from Labrador lakes and reservoirs. Drs. Anderson and Planas advised on the applicability of this approach to understanding how fish communities respond to anthropogenic or natural environmental changes.

(iii) DATA ANALYSIS

Marie-Julie Roux conducted all stable isotopes analysis of fish tissue and plankton samples used in the present research, and was actively involved in samples collection and preparation pertaining to Hg analysis in biota and water samples. Marie-Julie Roux was responsible for gathering and synthesising data on all Labrador study sites. Marie-Julie Roux conducted all data analysis involved and used in this thesis research. Dr. M. Robin Anderson and Dr. Dolors Planas provided reviews, comments and suggestions on data analysis by Marie-Julie Roux.

(iv) MANUSCRIPT PREPARATION

Marie-Julie Roux is the principal author of the four research papers presented in this thesis. Marie-Julie Roux identified and developed the research approach used throughout this thesis. Marie-Julie Roux was alone responsible for conducting literature reviews and data analysis, and for preparing the four manuscripts that form this thesis. Dr. M. Robin Anderson and Dr. Dolors Planas provided guidance, reviews, comments and suggestions in this process.

----- FIRST MOVEMENT:

A bi-dimensional approach to consumer feeding ecology and community structure

1. Chapter 1

BI-DIMENSIONAL FEEDING ECOLOGIES:

AN ANALYSIS OF VERTICAL AND HORIZONTAL RESOURCE USE BY FISH CONSUMERS

ABSTRACT

Recognizing the importance of spatial processes in sustaining consumer production, we propose to redefine consumer feeding ecology in two dimensions. Bi-dimensional feeding ecologies integrate horizontal (spatially-explicit) and vertical (trophic) energy flows to consumers. We demonstrate the relevance of this approach in a comparative stable isotope study of fish consumers among four lake ecosystems. We use variations in stable isotope ratios of nitrogen and carbon to study life-stage and among-lake patterns of fish trophic position (vertical resource use) and proportional reliance upon littoral-pelagic carbon sources (horizontal resource use), respectively. Variability in littoral-pelagic resource use and trophic omnivory are also contrasted. This analysis, supported by literature reviews of selected species biology, demonstrates that consumer ontogeny shapes vertical resource use as well as prey and habitat preferences in certain species, while ecosystem features affect horizontal resource use and the extent of vertical energy flows. The relative importance of species and ecosystem effects in fact distinguishes three bi-dimensional feeding strategies which we propose to classify under autecological types. Autecological types (Quis, Ubi and Aequivocus) describe the functional role of consumer species in two-dimensional space of ecosystems, and permit the formulation of assumptions relating to consumer flexibility in bi-dimensional resource use in the context of environmental variability. Bi-dimensional feeding ecologies therefore provide a conceptual basis for understanding ecosystem processes underlying community organization, and make explicit important dynamic links between species traits and ecosystem characteristics. As such, a bi-dimensional framework may serve to evaluate consumer species response to change or perturbations in their environment, and to address complex environmental issues like contaminant bioaccumulation. We argue that this intuitive, general approach can be applied across consumers and ecosystem types.

INTRODUCTION

In recent years, ecological research has seen the reaffirmation of the importance of spatial subsidies for consumer communities and entire food webs (Polis et al. 1997, Vadeboncoeur et al. 2002, Lundberg and Moberg 2003, Carpenter et al. 2005, Marczak et al. 2007). Operating in conjunction with trophic or vertical energy flows, spatial subsidies occur when spatially discrete carbon sources generate spatially distinct or horizontal energy flows at the consumer level (Fig 1-1).

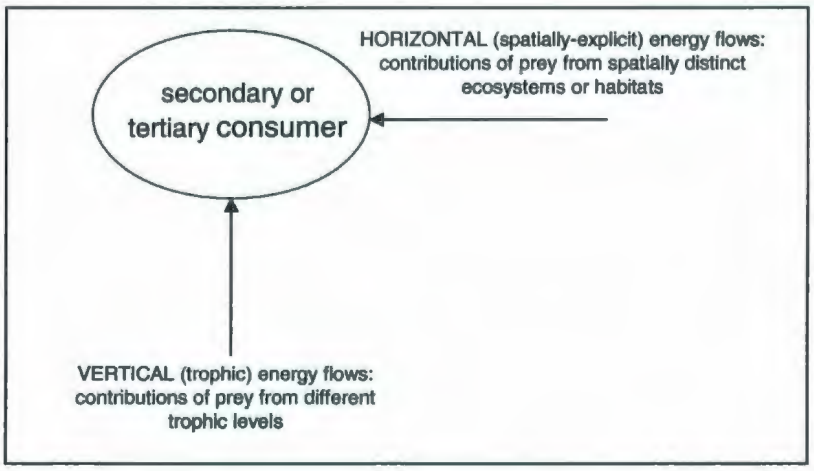

Fig. 1-1. Two-dimensional energy flows to consumers.

Horizontal foraging across spatial boundaries (i.e. between ecosystems in a landscape or between habitats within an ecosystem) is an important spatial process that can decouple consumer success from local constraints of productivity and prey dynamics (Polis et al. 1997, Schindler and Scheuerell 2002). Cross-ecosystem foraging by migrating consumers for example, serves to maintain their populations between less productive environments (i.e. summer breeding versus winter feeding grounds) (Polis et al. 1997). Similarly, cross-habitat foraging and allochtonous subsidies can sustain consumer populations in

ecosystems where *in situ* resources alone would not suffice (Nakano and Murakami 2001, Pace et al. 2004). Thus horizontal resource use by consumers has profound consequences on trophic interactions, on the direction of vertical energy flows (i.e. trophic cascades), and on the stability of consumer populations, communities and entire food webs (Polis and Strong 1996, Huxel and McCann 1998, Holt 2002, Rooney et al. 2006, Fagan et al. 2007).

Recognizing the intrinsic character of spatial processes at the consumer-level, we propose to redefine consumer feeding ecology in two dimensions. Bi-dimensional feeding ecologies link the vertical (trophic) and horizontal (spatial) energy flows that together support consumer production. We suggest that vertical resource use among trophic levels is primarily determined by consumer ontogeny. Horizontal resource use between spatially distinct habitats is assumed to be determined by both species and ecosystem characteristics (Polis et al. 1997, Roux et al. 2008, Schindler and Scheuerell 2002). Bi-dimensional feeding strategies therefore, should reflect a balance between species and ecosystem influences, and as such provide a functional measure of species-environment relationships.

We demonstrate the implications of this approach in a comparative stable isotope study of fish consumers from pristine lakes of Labrador, Canada. Lake ecosystems offer excellent environments to obtain comparative data with which to test ecological theory (Persson et al. 1992). Stable isotope ratios provide temporally-integrated representations of all energy pathways leading to an organism (Laymann et al. 2007). Thus they offer an excellent tool to trace consumer bi-dimensional resource utilization. Using stable isotopes of nitrogen and carbon as vertical trophic indicators and horizontal carbon source-flux tracers

respectively, we (i) estimate the vertical tophic position and horizontal reliance upon spatially distinct carbon sources in fish consumers, and (ii) assess how these parameters vary for each species among life-stages and lakes. Horizontal resource utilization here distinguishes between littoral and pelagic carbon sources in lakes. The bi-dimensional feeding ecologies of fish are thus depicted as variations in vertical (trophic) and horizontal (spatially explicit) resource utilization quantified by variations in stable isotope composition (Fig. 1-2). Comparisons among lakes and life-stages permit to measure the influence of ecosystems and species specific characteristics in determining bi-dimensional feeding strategies.

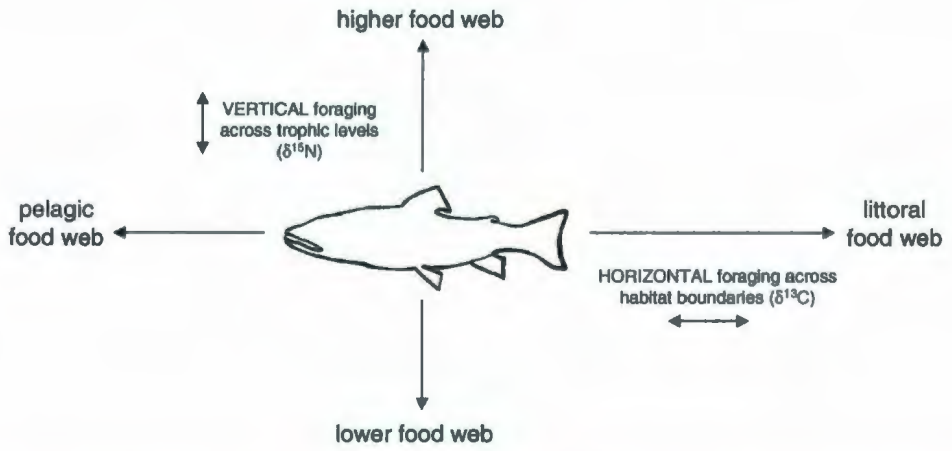

Fig. 1-2. Bi-dimensional feeding ecology of fish consumers. Vertical and horizontal resource use are quantified as variations in $\delta^{15}N$-estimates of trophic position (TrophP) and $\delta^{13}C$-estimates of percent reliance on littoral-pelagic carbon sources ($\%C_{LITT/PEL}$), respectively.

This comparative study confirms the importance of both vertical and horizontal resource use at the consumer level. Furthermore, it demonstrates that species and ecosystem effects delineate different bi-dimensional feeding strategies which we propose to classify under

three autecological types. This paper will define and demonstrate these autecological types and discuss their application for habitat and species conservation and management strategies.

MATERIAL AND METHODS

Study sites

Research was conducted in Labrador, Canada (Fig. 1-3). Study lakes were located in pristine areas remote from human settlements and point sources of anthropogenic pollution.

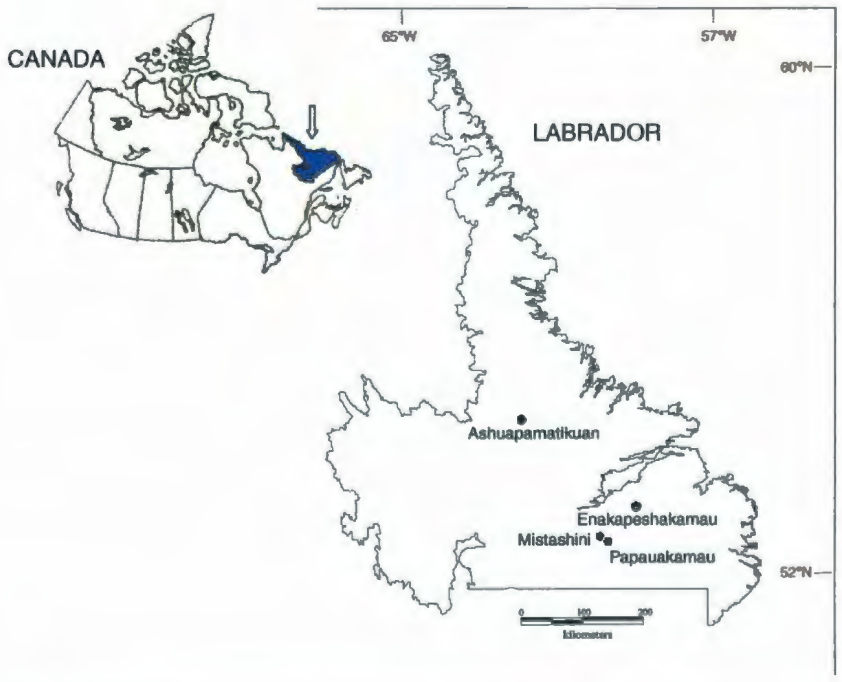

Fig. 1-3. Map of Canada and Labrador showing the location of the study lakes.

One site (Ashuapamatikuan Lake) was located in the 12,272km^2 Kanairiktok river system, while the other three (Enakapeshakamau Lake, Mistashini Lake and Papauakamau Lake) were part of the Eagle River watershed, draining over 10,500km^2 of the Labrador landscape (Anderson 1985). The three lakes in the Eagle river watershed had similar fish communities including Long Nose Sucker (*Catastomus catostomus* (Forster)), White Sucker (*Catastomus commersoni* (Lacépède)), Northern Pike (*Esox lucius* (Linnaeus)) and Brook Trout (*Salvelinus fontinalis* (Mitchill)). Ouananiche parr (*Salmo salar* (Linnaeus)) were also sampled in Enakapeshakamau lake. Ashuapamatikuan lake held a different fish community characterized by the absence of White Sucker and Brook Trout and the presence of White Fish (*Coregonus clupeaformis* (Mitchill)) and Lake Trout (*Salvelinus namaycush* (Walbaum)). The four study lakes drained east, were oligotrophic, supported relatively simple biological communities and differed by their morphometry (Table 1-1). Labrador is characterized by a cold continental climate with mean annual temperatures of -1.2°C (Environment Canada 2004b). The region is typically under snow cover from late October until late May to early June, during which time lakes are ice covered (Scruton 1984).

Field Sampling

Lakes were accessed by floatplane in July of 2002 and 2003, and sampled for fish (in both 2002 and 2003) and for water quality, periphyton, suspended particulate and plankton (in 2003 only). Lakes were physically characterized using GIS (for lake perimeter (LPeri), surface area (LArea), and drainage area (DArea). Maximum depth (Zmax) was recorded on-site as the deepest point measured over repeated depth transects. Two sampling stations were used to determine water column characteristics (pH and

temperature profiles with depth), to collect integrated photic zone water samples for pelagic chlorophyll *a* (Chla(pel)) and suspended particulate matter (SPM) determination, and to sample 53 to 99µm plankton in each lake. Rock surfaces were the principal littoral periphyton substrate in all study lakes. Periphyton was brushed from littoral rocks surfaces between 0.5 and 0.8m depth following the method described by Desrosiers et al. (2006a). Periphyton was collected from two distinct sampling locations in each lake.

Table 1-1. Physico-chemical characteristics and productivity indices (mean values) of the study lakes.

	Ashuapamatikuan	**Enakapeshakamau**	**Mistashini**	**Papauakamau**
Coordinates	54°39'N	53°15'N	52°46'N	52°41'N
	62°24'W	59°04'W	59°35'W	59°24'W
Watershed	Kanairiktok River	Eagle River	Eagle River	Eagle River
DArea (km^2)	3433	1240	276.5	323.4
LArea (km^2)	17.21	20.65	6.21	27.43
DRatio	199.48	60.05	44.52	11.79
LPeri (km)	27.75	54.43	10.15	43.94
PAratio	1.61	2.64	1.64	1.60
SDI	1.9	3.4	1.1	2.4
Zmax (m)	115	26	2	20
pH	6.3	6	5.9	5.8
Secchi (m)	5	7	1.5	2
SPM (mg/L)	0.14	0.21	0.93	1.55
Chla(pel) (µg/L)	0.67	0.82	1.94	2.68
Biomass(peri) (µg/cm^2)	1492	610	2464	1567
Chla(peri) (µg/cm^2)	1.82	0.39	1.81	1.95
%Chla(peri)	0.132	0.086	0.078	0.291

Legend: DArea= lake drainage area, LArea= lake surface area, DRatio=DArea/LArea, LPeri= lake perimeter, PAratio=LPeri/LArea, SDI=shoreline development index, Z_{max}=maximum depth, SPM=suspended particulate matter, Chla(pel)=pelagic chlorophyll-*a* concentrations, Biomass(peri)=periphyton biomass, Chla(peri)= periphyton chlorophyll-*a* concentrations, %Chla(peri)= (Chla(peri)/ Biomass(peri))*100 (for replicate samples).

Fish were collected using experimental gill nets (gangs of 5 nets of varying mesh size) set overnight in near and off shore areas. Small littoral fish were also collected using hand-

held dip-nets. Fork length, weight, sex and maturity stage were recorded on site for all fish. Fish were judged as sexually mature when fully developed gonads and/or gametes could be observed. Otherwise, fish were classified as immature (undeveloped gonads) or maturing. Stomach contents were recorded for piscivorous species. Contents were differentiated and categorized as either fish (identified to genus or species) or others. Fish specimens were sampled on-site for white (dorsal) muscle and aging structures (opercular bones (Suckers), scales (Brook Trout), and cleithra (Northern Pike). All samples were frozen on-site.

Laboratory Analysis

SPM concentrations were measured as dry weights. Periphyton biomass (Biomass(peri)) was estimated as ash free dry weight (AFDW). Pelagic and periphyton chlorophyll-*a* (Chla) was extracted overnight by soaking filters in 90% acetone at 4°C and in the dark. Chla concentrations were then measured as fluorescence on a Turner Designs TD10 fluorometer. Periphyton percent chlorophyll-*a* is the average of Chla(peri):Biomass(peri) ratios calculated for replicate periphyton filters, expressed as a percentage. Drainage ratio (DRatio) is the ratio of lake drainage area over lake surface area. Shoreline development index (SDI) measures a lake's degree of irregularity relative to a perfect circle and is calculated as: $SDI = LPeri/(2*\sqrt{(LArea*\pi)}$. Lake perimeter to lake area ratio (PAratio=LPeri/LArea) measures lake shape and littoral habitat dimensionality as a proportion of edge to interior. Fish were aged by C. Robertson at the Ontario Federation of Anglers and Hunters.

Stable isotope analysis

Fish, plankton, SPM and periphyton samples were lyophilised prior to stable isotope analysis. In fish, white muscle tissue samples were homogenized using an agate mortar and pestle. Stable isotope ratios of carbon and nitrogen were separately determined for fish samples (n=204) on a Finnigan MAT252 stable isotope ratios mass spectrometer interfaced to an elemental analyzer, at the stable isotope laboratory in the department of Earth Sciences, Memorial University. Carbon and nitrogen isotopic compositions were separately measured for primary producer (filter) samples (periphyton (n=16), SPM (n=16), and 53µm plankton (n=8)) on a continuous flow stable isotope ratio mass spectrometer (Isoprime, GV instruments) and elemental analyzer at GEOTOP laboratories, Université du Québec à Montréal. Plankton samples analyzed on both mass spectrometry systems and in both laboratories yielded similar isotopic ratios within ±0.18‰ for $\delta^{13}C$, and ±0.27‰ for $\delta^{15}N$. Stable isotopic compositions are measured as the ratio of the heavier to the lighter isotope of an element, and expressed as permil difference (delta notation (δ)) from the same ratio in a standard reference material (i.e. $\delta^{13}C_{fish} = [(({}^{13}C/{}^{12}C)_{fish} / ({}^{13}C/{}^{12}C)_{VPDB}) - 1] *10^3$). Values are reported relating to international standards: Vienna Pee Dee belemnite (VPDB) limestone for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. Working standards were LSVEC ($\delta^{13}C$ -46.48‰) and IAEA-CH-6 ($\delta^{13}C$ -10.43‰) for carbon, and IAEA-N-1 ($\delta^{15}N$ 0.43‰) and USGS-26 ($\delta^{15}N$ 53.62‰) for nitrogen. Overall standard deviation values for day-to-day isotope ratio measurements on a fish (*S. namaycush*) sample from Ashuapamatikuan Lake, were

equivalent to ±0.11‰ for $\delta^{13}C$ and ±0.09‰ for $\delta^{15}N$. Results for carbon and nitrogen elemental analysis were used to calculate sample C:N elemental ratios.

Stable Isotope Data

Mean isotopic compositions of periphyton and SPM +53μm plankton were used as littoral and pelagic isotopic baselines, respectively (Fig. 1-4). In each lake, the isotopic signatures of SPM and 53μm plankton were combined to yield a pelagic baseline composition and trophic position similar to that of littoral periphyton, which necessarily contains both primary producers and microbial consumers. Primary producers isotopic signatures vary both spatially and temporally within lakes. Herein, spatial variability was accounted for by distinguishing between littoral and pelagic habitats for sampling, and by replication within and between sampling locations. In boreal aquatic ecosystems, temporal variations in algal isotopic signatures can be negligible (Marty and Planas 2008). This is further expected in Labrador lakes that rarely if ever stratify (Scruton 1984). Based on this, we determined that the use of pelagic and littoral primary producers as isotopic baselines was adequate to measure trophic and littoral-pelagic dietary pathways in fish consumers in a comparative, rather than absolute, study.

In all lakes, the carbon isotope signatures of littoral and pelagic primary producers significantly differed (differences in $\delta^{13}C$ between littoral and pelagic baselines in Ashuapamatikuan lake: $t=-2.918$, $df=4$, $p=0.043$; Enakapeshakamau lake: $t=-4.809$, $df=3$, $p=0.017$; Mistashini lake: $t=-10.578$, $df=4$, $p<0.001$; Papauakamau lake: $t=-17.253$, $df=4$, $p<0.001$). This was expected from differential influence of physical forcing (turbulence)

on carbon availability and photosynthesis-related carbon isotope fractionation between littoral and pelagic habitats (France 1995, Hecky and Heisslein 1995).

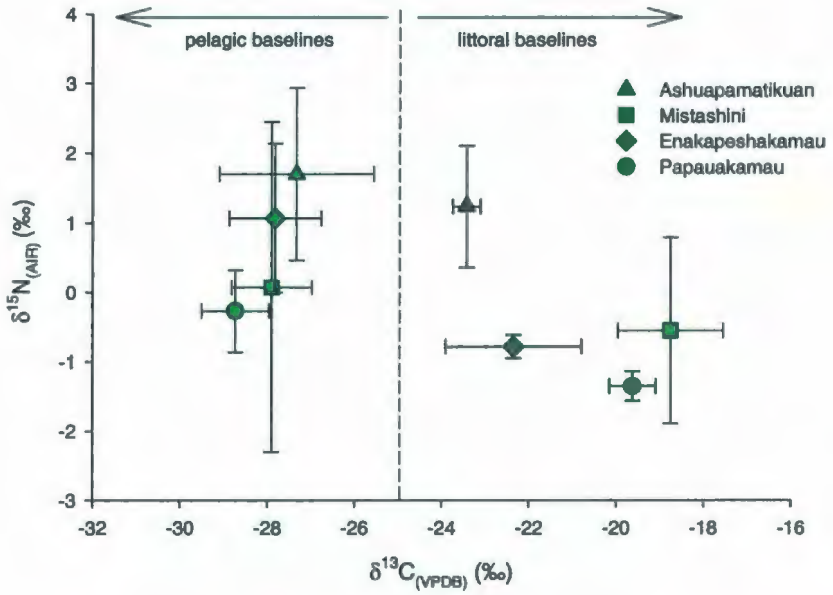

Fig. 1-4. Lake-specific carbon and nitrogen isotopic signals (mean±StdDev) for pelagic and littoral baselines organisms.

Significantly different carbon isotopic endpoints ($\delta^{13}C_{pelagic}$ and $\delta^{13}C_{littoral}$) were thus used in lake-specific carbon isotope mixing models (Fry and Sherr 1984) to estimate proportional reliance on littoral versus pelagic carbon sources in fish: $\%C_{LITT/PEL} = [(\delta^{13}C_{fish} - \delta^{13}C_{pelagic})/ (\delta^{13}C_{littoral} - \delta^{13}C_{pelagic})] * 100$. Of all fish samples (n=204), 11 had $\delta^{13}C$ values outside the range delimited by site-specific carbon isotopic endpoints, yielding negative or >100% estimates of proportional reliance on littoral carbon. These samples values were rounded to 0% (when negative) or 100% (when >100%) as done by Vander Zanden and Vadeboncoeur (2002). Our mixing model assumes no trophic

fractionation of carbon isotopes ($\Delta^{13}C$=0‰). Such a model was shown by Vander Zanden and Vadeboncoeur (2002) to correlate well with stomach content-derived estimates of zoobenthivory in north-temperate lakes fish populations. Fish $\delta^{13}C$ signatures were not related to fish C:N elemental ratios (n=204, F=0.631 p=0.428) or to lipid content estimated from C:N ratios (n=204, F=1.108 p=0.294) using the equation proposed by McConnaughey and McRoy (1979). Thus we applied no lipid-correction to our samples $\delta^{13}C$ values. The carbon isotopic signatures of profundal-benthic organisms were not measured in this study. Produndal-benthic primary consumers $\delta^{13}C$ have been shown to overlap those of pelagic zooplankton in Ontario and Quebec lakes (at ±-30‰) (Vander Zanden and Rasmussen 1999). This is also likely to be the case in our study lakes. In consequence, increasing reliance upon pelagic zooplankton (as indicated by decreasing $\%C_{LITT/PEL}$ values) may in some cases indicate increasing reliance upon profundal-benthic invertebrates instead.

Lake-specific nitrogen isotopic baselines were used to estimate fish trophic position (TrophP) assuming a trophic fractionation for nitrogen isotopes ($\Delta^{15}N$) equivalent to +3.4‰ (Post 2002a): $TrophP = \alpha + (\delta^{15}N_{fish} - \delta^{15}N_{pelagic}) / \Delta^{15}N$ (where α is the trophic position of baseline organisms, here equal to 1). Baseline $\delta^{15}N$ signatures did not differ between lakes (for littoral baselines: n=8, $F_{3,4}$=3.781, p=0.116; for pelagic baselines: n=14, $F_{3,10}$=1.194, p=0.361) or between littoral and pelagic habitats within lakes (for Ashuapamatikuan: t=0.465, df=4, p=0.666; Enakapeshakamau: t=2.303, df=3, p=0.105; Mistashini: t=0.334, df=4, p=0.755; and Papauakamau: t=2.363, df=3, p=0.099) (Fig. 1-4).

Data Selection

Fish species

Of the seven species of fish caught in our study lakes, four (Brook Trout (BT), Long Nose Sucker (LNS), Northern Pike (NP), and White Sucker (WS)) were selected for this study. These species were sampled in three or four study lakes and in wide-enough size ranges to allow for size-class differentiations and comparison. A total of 204 fishes were considered. Fish populations were size-structured for analysis using species-specific biological data (Scott and Crossman 1998). *A priori* defined size-classes were later adjusted to fit age data according to the following criteria. For every species, size class I (scI) represents 0 to 2+ year(s) individuals, size class II (scII) comprises average-size fish, and size class III (scIII) corresponds to bigger-than-average size fish. Species-specific size ranges for the three size classes are shown in Table 1-2.

Table 1-2. Species specific size ranges (fork length) for each size class.

Species	Size class	Size range (mm)
Brook Trout (BT)	I	≤100
(*Salvelinus fontinalis*)	II	101-279
	III	≥280
Long Nose Sucker (LNS)	I	≤100
(*Catostomus catostomus*)	II	101-349
	III	≥350
Northern Pike (NP)	I	≤300
(*Esox lucius*)	II	301-699
	III	≥700
White Sucker (WS)	I	≤100
(*Catostomus commersoni*)	II	101-379
	III	≥380

Lake characteristics

Five lake characteristics (LArea, DRatio, PAratio, Chla(pel) and %Chla(peri)) were selected from measured lake parameters (Table 1-1) to study the influence of ecosystem features on vertical trophic position and horizontal littoral-pelagic resource use in fish consumers. Selected characteristics were chosen to be representative of (i) lake shape and littoral–pelagic habitat physiognomy, (ii) watershed influence, and (iii) littoral-pelagic habitats primary productivity, whilst minimizing co-variation among variables. %Chla(peri) was thus preferred to Chla(peri) concentrations as an indicator of littoral productivity, the later being highly correlated to lake PAratio ($n=4$ $r=-0.998$ $p=0.002$). Remaining correlations between selected lake variables were not statistically significant.

Data analysis

"Population" refers to all fish from a given species sampled in a lake. "Community" applies to the entire fish assemblage (i.e. all fish species) sampled in a lake. "Ontogeny" is the combination of species-specific life-history and growth-related traits.

Stable isotope estimates of trophic position (TrophP) are used as indicators of vertical resource use among trophic levels. Stable isotope estimates of proportional reliance on littoral versus pelagic carbon sources ($\%C_{LITT/PEL}$) are used as indicators of horizontal cross-habitat resource use within lakes. We compared mean estimates of TrophP and $\%C_{LITT/PEL}$ among life-stages and lakes in each species. Variability (variances) around mean estimates of TrophP and $\%C_{LITT/PEL}$ were also compared and used as measurements of trophic omnivory (variability in TrophP) and littoral-pelagic feeding diversity (variability in $\%C_{LITT/PEL}$). Lake-specific slopes of TrophP and $\%C_{LITT/PEL}$ versus body size relationships were contrasted to confirm among lake differences in life-stage

patterns. Because $\%C_{LITT/PEL}$ varied nonlinearly with body size, we used species-specific mean fork length as a break point for two separate slopes analysis: a first one for juvenile to average size fish, and a second one for average size fish to larger size adults. For clarity and generalization, results are presented and discussed under life-stage and lake-to-lake patterns, along with a literature review of selected species biology. Life-stage patterns describe species and population specific variations in vertical and horizontal resource use among size classes. Lake-to-lake patterns describe variations in vertical and horizontal resource use among lake ecosystems, for each species and size class.

Statistical analysis

Among-lake and size-class variations in TrophP and $\%C_{LITT/PEL}$ were tested as differences in means using one-way ANOVAs. Scheffe's test was used to identify significant pairwise differences. Variances were compared using Levenes's test for equality of variance. Lake-specific slopes of TrophP and $\%C_{LITT/PEL}$ versus fork length relationships were compared using GLM procedure. Pearson correlation was used to determine whether among-lake differences in fish TrophP and $\%C_{LITT/PEL}$ were related to selected lake characteristics. Minitab® software was used to verify residuals assumptions, to compare variances (Levenes' tests) and to generate Pearson correlation matrices with p-values. All other statistical procedures (differences in means, pairwise comparisons and GLM procedure) were carried out on SYSTAT® software (Wilkinson 2001).

RESULTS AND DISCUSSION

Lake ecosystems (Table 1-1)

The study lakes were not stratified (no distinct thermoclines were observed). Papauakamau was the most productive and largest of the study lakes and had the smallest DRatio. Mistashini was smaller and shallower than other lakes. Limited shoreline development (SDI) and important periphyton biomass (Biomass(peri)) with low chlorophyll-a concentrations Chla(peri) were also distinctive traits of Mistashini lake. Northermost Ashuapamatikuan lake differed by its great depth, extensive Darea, largest Dratio, and lower pelagic primary productivity (lowest Chla(pel) and SPM concentrations were observed in this lake). With comparatively little SDI, Ashuapamatikuan lake had the second most productive littoral zone (after Papauakamau) as %Chla(peri). Enakapeshakamau lake had clear waters and important littoral habitat dimensionality as indicated by largest SDI and PAratio values. Its littoral area however bore the lowest Biomass(peri) and Chla(peri) concentrations of all study lakes. Lower SPM and Chla(pel) concentrations similar to Ashuapamatikuan also characterized Enakapeshakamau lake.

Fish consumers

Sample sizes, mean age and size structure (with ranges), maturity stage (as percent sexually immature individuals) and isotopic data are presented for each fish species in tables 1-3 to 1-6. Mean age and fork length by species only differed among lakes in Brook Trout (for Age: n=34, $F_{2,31}$=8.14, p=0.001; for FL: n=38, $F_{2,35}$=27.44, p<0.001) (Table 1-3). Papauakamau and Mistashini lake samples only included scIII (≥280mm) individuals, thus hampering among-population comparisons due to size and age bias in

this species. Mean age and fork length were otherwise comparable across Northern Pike, White Sucker and Long Nose Sucker populations (Tables 1-4 , 1-5 and 1-6).

Table 1-3. Brook Trout morphometrics and stable isotope data.

		n	Age	A-range	FL (mm)	FL-range	%SxI	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$
species total		38	4+	1-7	275	84-557			2.7		54
Enaka	pop	27	3+	1-6	214	84-349	22	6.2±0.1	2.5	-24.3±0.2	65
	scI	2	1+	1	85	84-85	50	5.2±0.0	2.2	-26.0±1.6	37
	scII	19	3+	2-6	194	108-278	21	6.2±0.1	2.5	-24.2±0.2	65
	scIII	6	4+	4-6	323	290-349	17	6.5±0.1	2.6	-23.8±0.2	73
Mista	pop	8	5+	4-7	429	283-557	0	6.8±0.2	3.0	-25.2±0.3	29
	scI	0									
	scII	0									
	scIII	8	5+	4-7	429	283-557	0	6.8±0.2	3.0	-25.2±0.3	29
Papau	pop	3	5+	5-6	403	320-450	0	8.0±0.1	3.4	-26.2±0.2	28
	scI	0									
	scII	0									
	scIII	3	5+	5-6	403	320-450	0	8.0±0.1	3.4	-26.2±0.2	28

Enaka=Enakapeshakamau Lake, Mista=Mistashini Lake, Papau= Papauakamau Lake. pop=population, sc=size class, A-range=age range, FL=fork length, %SxI=percent sexually immature fish, TrophP=trophic position, $\%C_{LITT/PEL}$=percent reliance on littoral versus pelagic carbon. Mean values or means ± SE.

Table 1-4. Northern Pike morphometrics and stable isotope data.

		n	Age	A-range	FL (mm)	FL-range	%SxI	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$
species total		54	7+	0-15	601	88-985			3.3		38
Ashua	pop	18	7+	2-12	619	135-840	17	9.5±0.2	3.3	-25.8±0.3	39
	scI	1	2+	2	135	135	0	7.0	3.0	-22.9	100
	scII	10	5+	3-11	557	435-690	20	9.4±0.3	3.3	-26.2±0.4	31
	scIII	7	9+	7-12	776	722-840	14	10±0.1	3.4	-25.7±0.1	43
Enaka	pop	5	4+	1-7	477	192-732	40	7.6±0.5	2.9	-24.0±0.1	70
	scI	1	1+		192		100	6.2	3.0	-24.3	65
	scII	3	5+	3-7	487	306-655	33	7.7±0.4	3.0	-23.9±0.2	72
	scIII	1	6+		732		0	8.7	3.0	-24.0	69
Mista	pop	21	7+	0-15	562	88-985	29	7.6±0.4	3.2	-25.0±0.2	32
	scI	6	1+	0-2	165	88-222	100	5.1±0.3	2.5	-24.4±0.2	38
	scII	8	8+	6-10	604	515-663	0	8.5±0.1	3.5	-25.7±0.4	24
	scIII	7	11+	8-15	855	773-985	0	8.8±0.1	3.6	-24.6±0.2	36
Papau	pop	10	8+	3-14	715	330-930	20	9.3±0.2	3.8	-25.6±0.3	35
	scI	0									
	scII	3	4+	3-6	430	330-610	67	8.6±0.6	3.6	-26.1±0.8	29
	scIII	7	10+	5-14	837	700-930	0	9.6±0.1	3.9	-25.4±0.1	37

Ashua=Ashuapamatikuan Lake, Enaka=Enakapeshakamau Lake, Mista=Mistashini Lake, Papau= Papauakamau Lake. (See complete legend Table 1-3)

Table 1-5. White Sucker morphometrics and stable isotope data.

		n	Age	A-range	FL (mm)	FL-range	%SxI	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$
species total		54	13+	≤2-28	378	65-570			2.7		47
Enaka	pop	19	11+	3-27	359	147-570	21	5.9±0.1	2.4	-24.3±0.2	64
	scI	0									
	scII	10	8+	3-12	290	147-370	30	5.9±0.1	2.4	-24.5±0.2	60
	scIII	9	16+	12-27	436	386-570	11	5.8±0.1	2.4	-24.1±0.2	68
Mista	pop	21	13+	4-28	370	65-485	19	5.8±0.1	2.7	-24.5±0.2	37
	scI	1	≤2+		65		100	4.5	2.0	-25.8	23
	scII	9	7+	4-11	326	205-369	33	6.0±0.2	2.7	-24.3±0.5	40
	scIII	11	18+	9-28	434	393-485	0	5.8±0.1	2.7	-24.6±0.2	37
Papau	pop	14	14+	6-20	414	335-445	0	6.8±0.1	3.1	-25.1±0.3	40
	scI	0									
	scII	2	10+	6-14	353	335-371	0	6.7±0.4	3.0	-26.1±0.1	29
	scIII	12	15+	11-20	424	388-445	0	6.8±0.1	3.1	-25.0±0.4	41

(See legend Table 1-3)

Table 1-6. Long Nose Sucker morphometrics and stable isotope data.

		n	Age	A-range	FL (mm)	FL-range	%SxI	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$
species total		58	12+	1-35	331	65-559			2.6		44
Ashua	pop	18	15+	1-35	343	67-559	17	7.0±0.1	2.6	-26.2±0.5	36
	scI	4	1+	1-2	70	67-72	75	6.8±0.1	2.5	-24.5±0.7	72
	scII	4	5+	2-7	247	105-305	0	7.3±0.5	2.7	-25.8±1.2	31
	scIII	10	23+	12-35	491	429-559	0	6.9±0.2	2.5	-27.0±0.5	23
Enaka	pop	17	11+	4-18	337	119-493	47	5.7±0.1	2.4	-25.0±0.2	52
	scI	0									
	scII	8	7+	4-13	227	119-335	100	5.7±0.1	2.4	-24.9±0.3	53
	scIII	9	14+	12-18	435	400-493	0	5.7±0.1	2.4	-25.0±0.2	51
Mista	pop	14	13+	1-29	347	65-525	36	5.6±0.2	2.6	-24.2±0.4	40
	scI	3	1+	1-2	70	65-75	100	5.1±0.4	2.5	-25.9±0.5	22
	scII	3	6+	2-9	251	106-324	67	6.2±0.6	2.8	-22.2±0.8	63
	scIII	8	19+	12-29	487	440-525	0	5.5±0.2	2.6	-24.4±0.2	38
Papau	pop	9	9+	1-18	269	70-457	56	6.3±0.3	2.9	-24.2±0.4	50
	scI	3	1+	1-2	72	70-75	100	5.6±0.3	2.7	-25.0±0.6	41
	scII	2	4+	4	221	210-331	100	7.1±0.5	3.2	-22.7±0.4	66
	scIII	4	15+	13-18	441	428-457	0	6.5±0.3	3.0	-24.3±0.5	48

(See legend Table 1-3)

Stomach contents

Invertebrates dominated in BT stomachs except for scIII BT in Enakapeshakamau lake, where fish remains and field mice each represented 33% of non-empty BT stomachs. NP stomachs contained mostly fish. *Catostomus* sp. (WS and/or LNS) dominated in NP stomachs from Papauakamau and Enakapeshakamau lakes (representing 60% and 100% of non-empty stomachs respectively), as well as in scI NP stomachs from Mistashini lake

(50% of non-empty stomachs). Some BT were found in scII and scIII Pike stomachs in Mistashini and Papauakamau lakes (50% and 67% of non-empty stomachs respectively). 100% of non-empty NP stomachs in Ashuapamatikuan lake contained Lake Trout.

Bi-dimensional feeding ecologies

Figure 1-5 shows species and population-specific size-class variations in vertical trophic position (5a to 5d) and horizontal reliance upon littoral-pelagic carbon sources (5e to 5h) in fish consumers.

Life-stage patterns in VERTICAL resource use and trophic omnivory

Life-stage patterns were particularly relevant to vertical resource use in fish consumers. For each species, size-class transitions – or absence of transitions - in trophic position were similar among populations (Fig. 1-5a to 1-5d).

Trophic position increased with size in Brook Trout from Enapeshakamau Lake (n=27, $F_{2,24}$=6.15, p=0.007) and in Mistashini, Papauakamau and Ashuapamatikuan populations of Northern Pike (for Mistashini NP: n=21, $F_{2,18}$=150.65, p<0.001; Papauakamau NP: n=10, $F_{1,8}$=7.97, p=0.022; Ashuapamatikuan NP: n=18, $F_{2,15}$=9.26, p=0.002) (Fig. 1-5a and 1-5b). A similar pattern for NP in Enakapeshakamau lake lacked statistical significance likely due to a small sample number (n=5) (Fig. 1-5b). The increase in trophic position with body size in BT and NP indicates a change in diet composition with growth, or a transition from feeding at a lower trophic level in scI to a higher trophic level in scIII. In NP, this transition was clear-cut and similar between populations and corresponded to an increase in nitrogen isotopic signals of +2.49‰ to +3.68‰ from scI to scIII, depending on lake (mean trophic enrichment of +3.06‰ across populations) (Table 1-4).

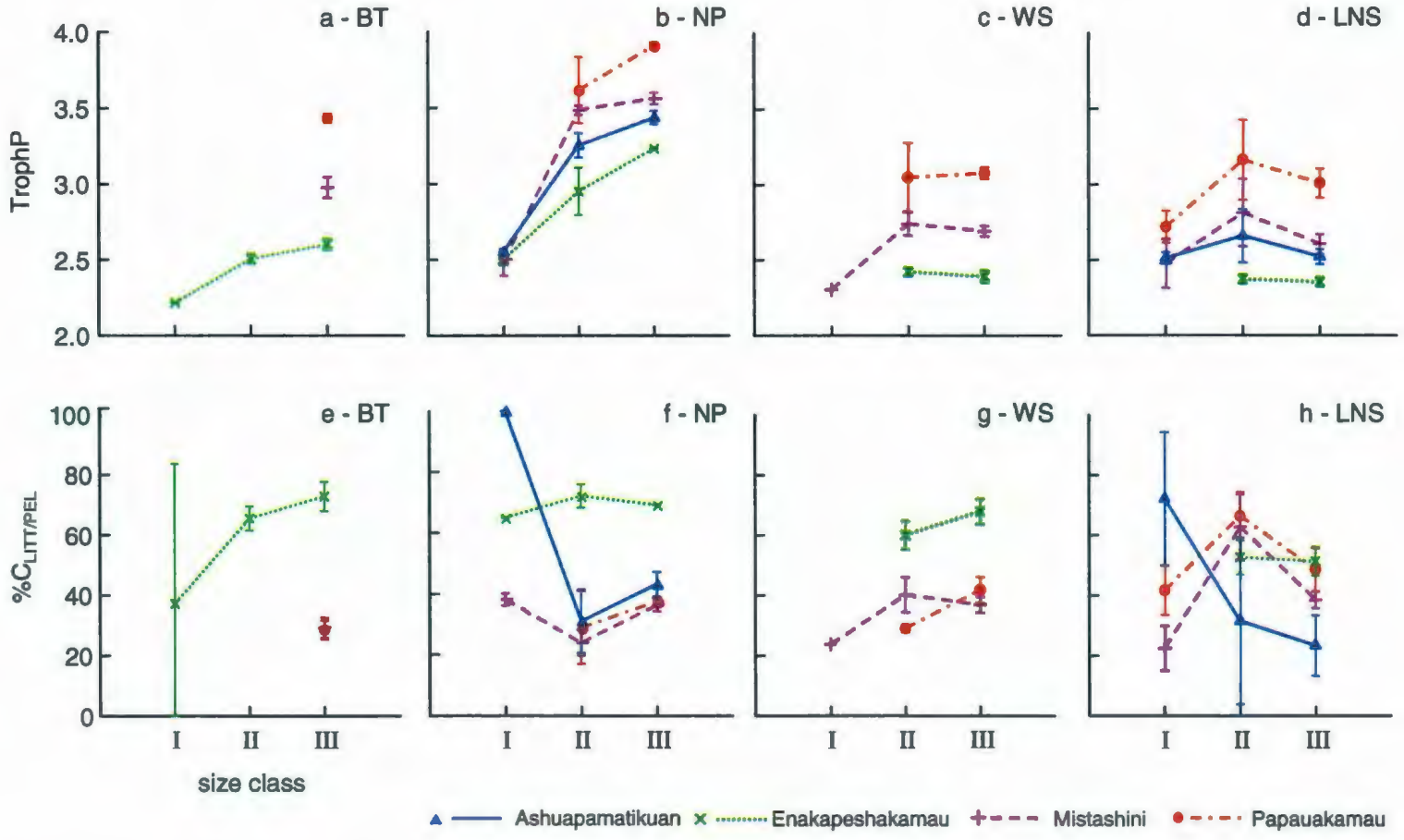

Figure 1-5. Size-class variations in TrophP (5a to 5d) and $\%C_{LITT/PEL}$ (5e to 5h) for Brook Trout (BT), Northern Pike (NP), White Sucker (WS) and Long Nose Sucker (LNS) across the study lakes. Size-class means (± SE) are linked in left to right order to emphasize species and population specific transitions with increasing size.

Fish dominate (>90%) NP diet once it reaches ≈50mm in length (Scott and Crossman 1998). The observed increase in NP $\delta^{15}N$ and trophic position thereby constitutes a change in vertical resource use that is consistent with the species ontogeny (i.e. switch from an invertebrate diet to an essentially piscivorous diet early in life (Hunt and Carbine 1951, Frost 1954, Scott and Crossman 1998)). The prevalence of fish in adult NP diet also tends to be strongest in lakes where prey fish species are present (Beaudoin et al. 1999). Most lakes in southern and central Labrador, including the study lakes, have well developed prey fish communities (Black et al. 1986).

In Enakapeshakamau BT (the only BT population where size-class variations could be evaluated), the increase in trophic position was comparatively smaller and did not constitute a real change in trophic level with increasing size (trophic shift in nitrogen isotopes from scI to scIII of +1.31‰ only) (Table 1-3). This suggests some degree of consistency in BT diet throughout life-stages, paralleled by the occasional contribution of fish and small terrestrial mammals to the diet of larger size individuals. Fish and mice (*Microtus*) were indeed observed in the stomachs of scIII BT but were absent in smaller size classes. Power et al. (2002b) found a similar relationship between Brook char $\delta^{15}N$ signatures and fork length, which based on stomach content analysis, reflected a shift towards piscivory with increasing size. BT are known as omnivores (though primarily carnivorous) that consume a broad diversity of organisms, from plant remains to aquatic and terrestrial insects and larvae, worms, leeches, crustaceans, small fish and small terrestrial mammals (Scott and Crossman 1998). BT piscivory however, was shown by Lacasse and Magnan (1992) to be related to littoral habitat characteristics as these influence prey-fish availability. This suggests that changes in vertical resource use with

size in BT are more opportunistic than determined by the species ontogeny. The inclusion of prey such as mice in the diet, which is permitted by an increase in mouth gape with growth, still relates to ontogenetic changes in morphology and foraging abilities (Galarowicz and Wahl 2005).

White Sucker and Long Nose Sucker populations were characterized by a lack of significant trophic transitions among size classes (Fig. 1-5c and 1-5d). Adult stages (scII and scIII) of both species fed on similar trophic levels in all populations. Only in Papauakamau lake LNS did trophic position barely differed among size classes (n=9, $F_{2,6}$=5.07, p=0.051). A higher mean trophic position characterized scII LNS in this lake, even though pairwise comparisons yielded no significant differences (Fig. 1-5d). This pattern was supported by the observation of significant linear relationships between fork length and trophic position in 65 to 335mm LNS (Fig. 1-7c). Sayigh and Morin (1986) have shown that algae/periphyton dominate the diet of small (<170mm) LNS, while adults have a net preference for benthic invertebrates. Such dietary transition would explain the pattern of increasing trophic position from scI to average-size LNS in Papauakamau and Mistashini lakes (Fig. 1-7c). It also demonstrates the occurrence of a change in vertical resource use determined by ontogeny in this species. In WS, the observation of dietary transitions between juveniles and average-size adults was precluded by the absence of scI fish in most populations (Fig. 1-5c).

Trophic omnivory was similar among size classes in all species and populations, with the exception of NP in Papauakamau lake. Greater variability in trophic position characterized average size (scII) NP relative to larger (scIII) adults in this population (n=10, W=18.597, p=0.003) (Fig. 1-5b). We suggest that this pattern is related to size-

selective predation between the two size classes and/or caused by dietary overlap and intra-specific competition. Intra specific competition would likely impose greater prey type and size variability in scII NP, relative to larger and competitively advantaged scIII individuals (Persson and Bronmark 2002).

Life-stage patterns in HORIZONTAL resource use and feeding diversity

Variations in horizontal littoral-pelagic resource use among size classes were generally population-specific (Fig. 1-5e to 1-5h). Littoral-pelagic feeding diversity did not differ among size classes in all species. Horizontal resource use by fish consumers therefore appear to be relatively independent of species ontogeny.

Littoral resource use increased with size in Enakapeshakamau Brook Trout, from a mean of 37% in scI to 72% in scIII ($n=8$, $F_{1,6}=6.13$, $p=0.048$). Comparatively lower reliance on littoral carbon in scIII BT in Papauakamau and Mistashini populations however, suggest that the life-stage pattern observed in Enakapeshakamau lake was population specific (Fig. 1-5e). Since BT is an opportunistic, primarily invertebrate feeder that will select prey based on size and availability (Allan 1981, Lacasse and Magnan 1992, Hilderbrand and Kershner 2004, Thorne 2004) life-stage transitions in littoral-pelagic foraging are likely independent of BT ontogeny.

In Northern Pike, littoral-pelagic foraging only differed among size classes in the Mistashini population ($n=21$, $F_{2,18}=7.07$ $p=0.005$) (Fig. 1-5f). Littoral contributions were significantly lower in scII (mean of 24%) relative to scI (38%) and scIII (36%) NP in this lake (Fig. 1-5f). Similar patterns of lower reliance upon littoral carbon in scII individuals were observed in Papauakamau and Ashuapamatikuan populations, though without statistical significance (Fig. 1-5f). This was further corroborated by negative linear

relationships between littoral resource use and body size in ≤601mm NP in Mistashini and Ashuapamatikuan lakes (Fig. 1-7). Like differences in trophic omnivory between adult size classes, the pattern of decreasing littoral resource use from juvenile to average-size NP is probably related to intra-specific competitive interactions. Strong intra-specific competition has been shown to cause the spatial segregation of size classes in fish as a means to sustain growth rates in more vulnerable (i.e. juvenile) individuals (Werner et al. 1977, Werner et al. 1983). NP is a littoral species and predator, favoring warm vegetated areas/bays of lakes and rivers (Scott and Crossman 1998). Mistashini is a small, circular lake with comparatively limited littoral habitat dimensionality as shoreline development (Table 1-1). Physical constraints on littoral habitat availability in Mistashini may have contributed to enhance intra-specific interactions in this NP population, thus explaining the significant reduction in littoral resource use in average size (scII) adults. This suggests that horizontal resource use is relatively constant throughout NP ontogeny, but is sensitive to physical ecosystem structure (i.e. preferred habitat dimensionality) as this determines the intensity of intra-specific interactions.

In all White Sucker populations, there were no significant littoral-pelagic dietary transitions among size classes. Benthic and pelagic invertebrates both contribute to the diet of WS and a broad flexibility in feeding habits and in benthic-pelagic resource use characterize the species (Ahlgren 1990, Logan et al. 1991, Scott and Crossman 1998, Saint-Jacques et al. 2000). Lalancette (1977) reported that zooplankton dominate the diet of young-of-the-year WS, while age ≥1 individuals have diversified diets mostly consisting of benthic invertebrates. The observation of such dietary transition was

precluded by the absence of scI WS in our sample (only one juvenile (scI) WS was collected in Mistashini lake). Thus within the size range available to our study, horizontal resource use by WS was independent of the species ontogeny.

In Long Nose Sucker, variations in horizontal littoral-pelagic resource use among size classes were clearly population specific. LNS littoral-pelagic resource use differed among size classes in Mistashini lake (n=14, $F_{2,11}$=14.53, p=0.001). Reliance upon littoral carbon was higher in scII (mean of 63%) relative to scI (mean of 22%) and scIII LNS (mean of 38%) in this population. A similar pattern in Papauakamau lake lacked statistical significance (Fig. 1-5h). In Ashuapamatikuan lake, LNS was characterized by a distinctive pattern of decreasing littoral resource use with increasing size (Fig. 1-5h). Littoral resource use was greater in scI (mean of 72%) relative to scIII adults (mean of 23%) in this population (n=14, $F_{1,12}$=6.66, p=0.024). The lake-specific character of life stage patterns in horizontal resource use by LNS, was further confirmed by linear relationships of fork length and reliance on littoral-pelagic carbon (Fig. 1-7b). Littoral resource use was positively related to body size in ≤331mm LNS in Mistashini and Papauakamau populations, but varied negatively in Ashuapamatikuan lake (Fig. 1-7b). Few studies have looked into life-stage variations in LNS diet. Like WS, the species is probably characterized by growth-related dietary transitions occurring at earlier life-stages than represented in our sample size-range (i.e. diet switches simultaneous with ontogenetic changes in feeding morphology, such as mouth reposition from terminal to ventral position (Scott and Crossman 1998)). The pattern of decreasing littoral resource use with increasing size observed in the Ashuapamatikuan lake population, is consistent

with the switch from a periphyton diet (in <170mm LNS) to a benthic invertebrate diet (in larger, sexually mature individuals) documented by Sayigh and Morin (1986) (assuming that greater reliance on pelagic carbon sources reflect greater reliance on profundal-benthic carbon sources by adult LNS in this lake (see material and methods section)) (Fig. 1-5h and 1-6b). This transition may constitute an ontogenetic shift in horizontal resource use driven by prey and habitat preferences, yet permitted by the physical extent of pelagic and profundal-benthic habitats in this lake (see Table 1-1) and by the absence of benthic competitors (such as the White Sucker). In contrast, littoral contributions were minimized for juvenile (scI) LNS in Papauakamau and Mistashini lakes (Fig. 1-5h and 1-6b).

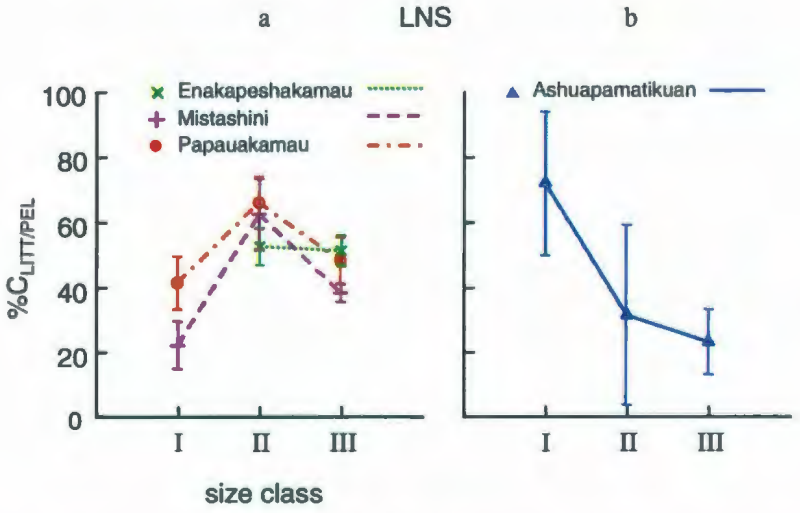

Fig. 1-6. Life-stage transitions in $\%C_{LITT/PEL}$ in LNS: distinction between (a) three sympatric populations and (b) an allopatric population.

Similar life-stage patterns of littoral-pelagic resource use characterized LNS in Mistashini, Papauakamau and Enakapeshakamau lakes, where the species was found to co-occur with the White Sucker, another benthivorous fish (Fig. 1-6a). This suggests that

life-stage patterns of horizontal resource use are determined by ontogenetic prey and habitat preferences in LNS, whilst being influenced by the physical characteristics of lake ecosystems and differences in community composition.

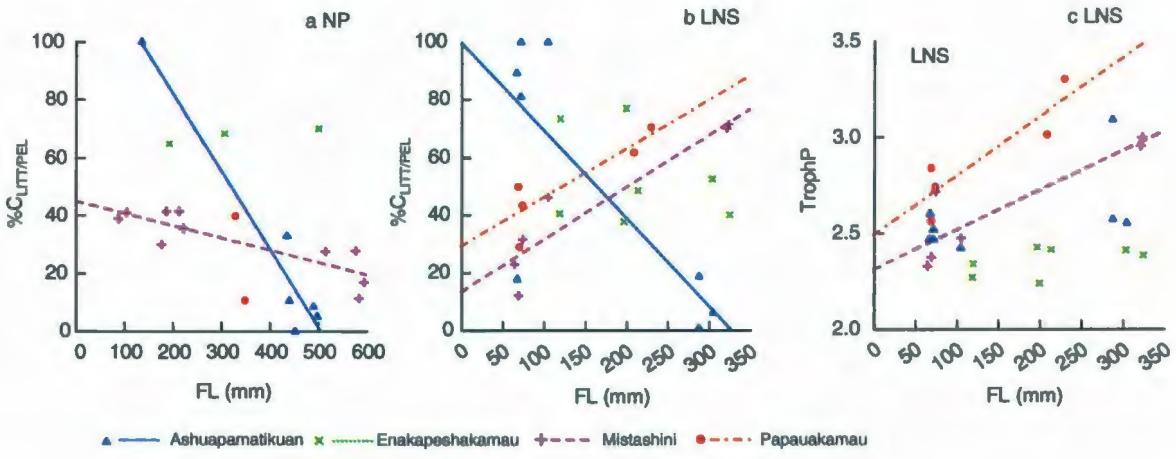

Fig. 1-7. Significant lake-to-lake differences in life-stage patterns. (a) $\%C_{LITT/PEL}$-FL relationships in ≤601mm (88-595mm) NP (Ashua: $\%C_{LITT/PEL}$=136 - 0,268FL (p=0.002, r^2=0.93), Enaka: $\%C_{LITT/PEL}$=62,5 + 0,0158FL (p>0.05, r^2=0.88), Mista: $\%C_{LITT/PEL}$=44,9 - 0,0424FL (p=0.002, r^2=0.73), Papau: (insufficient data)). (b) $\%C_{LITT/PEL}$-FL relationships in ≤331mm (65-325mm) LNS (Ashua: $\%C_{LITT/PEL}$=99,8 - 0,304FL (p=0.02, r^2=0.60) Enaka: $\%C_{LITT/PEL}$=65,3 - 0,0593FL (p>0.05, r^2=0.09), Mista: $\%C_{LITT/PEL}$=13,3 + 0,181FL (p=0.007, r^2=0.87), Papau: $\%C_{LITT/PEL}$=29,1 + 0,169FL (p=0.053, r^2=0.76)). (c) TrophP-FL relationships in ≤331mm LNS (Ashua: TrophP=2,42 + 0,00105FL (p>0.05, r^2=0.31), Enaka: TrophP=2,26 +0,000470FL (p>0.05, r^2=0.26), Mista: TrophP= 2,31 + 0,00207FL (p=0.016, r^2=0.80) Papau: TrophP=2,49 + 0,00308FL (p=0.041, r^2=0.80)).

Lake-to-Lake patterns in VERTICAL resource use and trophic omninory

Differences in vertical trophic position among lakes were only observed in adult size classes (scII and scIII) of all species. The trophic position of juvenile (scI) fish did not differ among lakes in NP and LNS (Fig. 1-5b to 1-5d). This indicates that life-history traits, more than ecosystem characteristics, determine vertical resource utilization in juvenile consumers.

Lake-to-lake patterns in trophic position were similar in all species. Average size fish (scII) had a lower mean trophic position in Enakapeshakamau lake (for scII NP: n=24, $F_{3,20}$=7.59, p=0.001, for scII WS: n=21, $F_{2,18}$=16.20, p<0.001; for scII LNS: n=17 $F_{3,13}$=9.85, p=0.001) (Fig. 1-5b to 1-5d). For scII NP and LNS, lower mean trophic positions in Enakapeshakamau lake were similar to those observed in Ashuapamatikuan lake (Fig.1-5b and 1-5d). Larger size (scIII) fish from all species had lower and higher mean trophic positions in Enakapeshakamau and Papauakamau lakes, respectively (for scIII BT: n=17, $F_{2,14}$=37.35, p<0.001; for scIII NP: n=22, $F_{3,18}$=45.65, p<0.001; for scIII WS: n=32, $F_{2,29}$=87.96, p<0.001; for scIII LNS: n=31, $F_{3,27}$=20.32, p<0.001) (Fig. 1-5a to 1-5d). Differences in vertical trophic position among lakes were not significantly correlated to any lake characteristics. Higher mean trophic positions in Papaukamau lake were however consistent with greater primary productivity at the base of littoral and pelagic habitats in this lake (Table 1-1). In contrast, lower mean trophic positions for fish in Enakapeshakamau lake were consistent with lower chlorophyll-a concentrations at the base of pelagic and littoral habitats (Table 1-1). This suggests that for a given lake ecosystem, the extent of vertical energy flows in fish consumers is related to primary productivity constraints at the food web base.

Trophic omnivory was similar among lakes for BT and NP but differed in WS and LNS (for WS: n=54, W=3.25, p=0.047; for LNS: n=58, W=3.27, p=0.028). Both sucker species had significantly reduced trophic omnivory in Enakapeshakamau lake. This pattern was related to strong reliance upon littoral resources by BT and NP in this lake (see Fig.1-5e and 1-5f). Community aggregation in the littoral habitat and comparatively lower primary productivity in Enakapeshakamau lake (see Table 1-1), may explain a

reduction in the range of prey types available to benthivorous WS and LNS via exploitative competition. Alternatively, it may have constrained both sucker species to feed on specific prey types as a result of increased predation risk (from NP) and/or interference competition (with BT).

Lake-to-lake patterns in HORIZONTAL resource use

All species evinced among-lake differences in littoral-pelagic resource use. This demonstrated the lake-specific character of horizontal cross-habitat foraging in fish consumers.

In scIII BT, littoral resource use was higher in Enakapeshakamau lake ($n=17$, $F_{2,14}=45.50$, $p<0.001$) (Fig. 1-5e) and positively correlated to the ratio of lake perimeter to lake area (PAratio) ($n=3$, $r=1.000$, $p=0.010$). This is consistent with the reported influence of littoral habitat complexity and prey abundances for determining diet composition in BT (Allan 1981, Lacasse and Magnan 1992). Important littoral habitat dimensionality in Enakapeshakamau lake (PAratio=2.64) provided for abundant littoral-benthic resources that were not limiting and/or allowed for within-habitat prey partitioning among fish consumers (i.e. selection of mice and fish prey by scIII BT).

In NP, reliance upon littoral carbon sources was greater in Ashuapamatikuan lake and lowest in Mistashini lake at the juvenile life stage (for scI NP: $n=8$, $F_{2,5}=87.05$, $p<0.001$) (Fig. 1-5f). Prey abundance and availability have been shown to influence prey selection in juvenile piscivores (Galarowicz and Wahl 2005, Galarowicz et al. 2006). We suggest that littoral-pelagic foraging by juvenile NP in the study lakes was similarly opportunistic. In adult size classes, NP reliance upon littoral resources was higher in Enakapeshakamau lake (in both scII and scIII) and lowest in Mistashini lake (in scII) (for

scII NP: n=24, $F_{3,20}$=3.55, p=0.033; for scIII NP: n=22, $F_{3,18}$=7.98, p=0.001) (Fig. 1-5f). As in BT, lake-to-lake differences in littoral-pelagic foraging by adult NP were positively correlated to lake PAratio (for scII NP: n=4, r=0.984, p=0.016; for scIII NP: n=4, r=0.977, p=0.023). This supports the hypothesis that cross-habitat foraging by top predators is influenced by habitat shape and complexity as this modulates foraging success and yields (Whitehead and Walde 1992, Sass et al. 2006). Important littoral habitat dimensionality in Enakapeshakamau lake would tend to favor prey aggregation, thus increasing foraging opportunities and yields for NP in the littoral. In contrast (and as discussed for life-stage patterns), limited littoral habitat dimensionality may work to intensify intra-specific interactions in NP and cause the spatial segregation of size classes. This probably explains lower reliance upon littoral resources by average size NP in Mistashini lake.

In adult WS, reliance upon littoral carbon sources was also higher in Enakapeshakamau relative to other lakes (for scII WS: n=21, $F_{2,18}$=6.31, p=0.008; for scIII WS: n=32, $F_{2,29}$=19.01, p<0.001) (Fig.1-5g). This pattern was negatively correlated to pelagic chlorophyll-a concentrations in average-size adults (for scII WS: n=3, r=-0.999, p=0.027). Increasing reliance upon pelagic carbon sources (and decreasing reliance on littoral foods) with increasing pelagic primary productivity, agrees with the opportunistic littoral-pelagic feeding behavior documented for WS (Ahlgren 1990, Scott and Crossman 1998, Saint-Jacques et al. 2000). Like BT, the species was shown to exert size-selective predation and to choose invertebrates based on their relative abundance (Lalancette 1977, Barton 1980, Saint-Jacques et al. 2000).

In LNS, littoral-pelagic resource use only differed among lakes in scIII individuals. Littoral resource use was higher in Enakapeshakamau lake relative to Ashuapamatikuan lake in this size class (n=31, $F_{3,27}$=3.63, p=0.025) (Fig. 1-5h). We have shown that life-stage patterns of horizontal resource in LNS were influenced by differences in community composition and physical ecosystem structure (Fig. 1-6). The same factors explained differences in horizontal foraging by LNS among the study lakes. LNS was sympatric to WS (a closely related benthivore (*Catostomidae* family)) in Papauakamau, Enakapeshakamau and Mistashini lakes. In Ashuapamatikuan lake, the LNS population was allopatric (i.e. absence of a closely related benthivore from the *Catostomidae* family). Reliance upon littoral resources in allopatric LNS was significantly higher than the average of sympatric populations at the juvenile life-stage (for scI LNS: n=10, t=-2.475, p=0.038) and significantly lower in larger adults (for scIII LNS: n=31, t=2.993, p=0.006) (Fig. 1-6a and 1-6b). LNS tends to favor cold waters and deeper areas of lakes while WS is usually found in warmer, shallow waters (Scott and Crossman 1998). Juvenile LNS however demonstrate a preference for littoral-benthic dietary items, mainly periphyton (Sayigh and Morin 1986). This underlines a potential for habitat overlap between LNS and WS at the juvenile life-stage. Such habitat overlap may be enhanced in shallow, cool water lakes of Labrador. Barton (1980) showed that reliance upon benthic invertebrates was higher in WS relative to LNS in sympatric populations of Paine lake, Alberta, where pelagic cladocerans then constituted 74% of LNS diet. This suggests that LNS alternatively feeds on pelagic zooplankton when sympatric with the WS. Inter-specific interactions with the WS may thus explain the pattern of lower reliance on littoral carbon sources by juvenile LNS in lakes where they co-occur. Alternatively, this pattern may

result from predation pressure from NP. Suckers (WS and LNS combined since they were generally indistinguishable as stomach contents) accounted for 45%, 60% and 100% of fish prey in NP stomachs of Mistashini, Papauakamau and Enakapeshakamau lakes, respectively. No suckers were found in the stomachs of NP in Ashuapamatikuan lake (due to the presence of alternative prey fish like juvenile Lake Trout). This indicated substantial predation pressure from NP on sucker species in sympatric lakes, which was limited or nil for allopatric LNS in Ashuapamatikuan lake. Changes in habitat use in response to predation-risk were shown for juvenile Bluegills (*Lepomis macrochirus*) in a small, circular pond (Werner et al. 1983). Risk of predation by NP therefore may have factored into lower reliance upon littoral carbon by juvenile LNS in Papauakamau and Mistashini lakes. In larger adults, lower reliance upon littoral resources in Ashuapamatikuan lake corresponded to an increase in profundal-benthic resource use permitted by the physical extent of the profundal-benthic habitat, and facilitated by the absence of WS. A difference in community composition, as a lake characteristic, thus explained lake-to-lake patterns of littoral resource use in juvenile LNS. In larger adults, this influence of community composition was paired to the influence of physical ecosystem structure.

Littoral-pelagic feeding diversity was similar between lakes for BT and WS, but differed in NP and LNS (for NP: n=54, W=6.04, p=0.001; for LNS: n=58, W=6.02, p=0.001). In both species, variability in littoral-pelagic resource was greater in Ashuapamatikuan lake (Fig.1-5f and 1-5h). This was related to the distinct physical characteristics (i.e. important depth) and community composition of Ashuapamatikuan lake. Its extensive pelagic and profundal-benthic habitats provided access to profundal-benthic carbon sources in adult

LNS. Its different community composition gave NP access to pelagic prey fish absent in other lakes, and facilitated littoral foraging by juvenile LNS under conditions of predation and competition release. Comparatively reduced littoral-pelagic feeding diversity in all size classes of LNS in Papauakamau, Enakapeshakamau and Mistashini lakes (see Fig.1-6), supports the idea that horizontal resource use was constrained by inter-specific interactions with WS and/or NP in these LNS populations.

SYNTHESIS AND IMPLICATIONS

Our study confirms that horizontal littoral-pelagic resource use together with vertical trophic foraging, is fundamental to the feeding ecology of fish consumers in lakes. We suggests that the complementary character of vertical and horizontal energy flows is a general feature of consumer-level feeding ecology.

Our comparative analysis of life-stage and lake-to-lake patterns has demonstrated (i) the importance of species-specific ontogeny in determining vertical resource utilization and prey or habitat preferences, and (ii) the central role of ecosystem specific characteristics (namely physical ecosystem structure, inter-habitat productivity and community composition and interactions) in determining horizontal resource use and the extent of vertical energy flows (i.e. species-specific maximum trophic positions and trophic omnivory). These results indicated that bi-dimensional feeding strategies are determined by "who" consumers are (species-specific features) and "where" consumers live (ecosystem specific characteristics), the relative importance of which is species-specific. This implies that life-history traits constrain the trophic role of consumers and the extent to which their resource use patterns across trophic levels and habitat boundaries can be

affected by the characteristics of their environment. As such, bi-dimensional feeding ecologies reflect dynamic links between species traits ("who") and ecosystem features ("where") and can be classified based on the relative importance of these effects. We propose to classify bi-dimensional feeding strategies into three autecological types: "Quis", "Ubi" and "Aequivocus". The *Quis* type represents consumers whose bi-dimensional feeding ecology is determined by ontogeny. The *Ubi* type represents consumers whose bi-dimensional feeding ecology is mainly shaped by ecosystem characteristics. The *Aequivocus* type corresponds to consumers whose bi-dimensional feeding ecology is reciprocally determined by species and ecosystem-specific features. Each of these autecological types were exemplified in our fish communities.

The Quis type was represented by Northern Pike, whose prey and habitat preferences were determined by ontogenetic metabolic requirements in prey profitability. The Quis type will include top-predators and species characterized by rigid life-history traits that are consistent among ecosystems. Comparative life-stage and lake-to-lake patterns in Northern Pike have shown that vertical resource use among trophic levels is strongly influenced by ontogeny in Quis type consumers. Horizontal littoral-pelagic habitat use was determined by ontogenetic preferences, community composition and intra-specific interactions whose intensity was influenced by physical ecosystem structure. This demonstrated that Quis type consumers will first compete for preferred or more profitable foraging habitat and food resources, prior to switching to an alternative habitat or becoming more opportunistic in food choices. In consequence, the bi-dimensional feeding strategies of Quis consumers will tend to remain similar between ecosystems, or vary predictably with certain ecosystem features.

The Ubi type was represented by Brook Trout and White Sucker in our study lakes. Ubi consumers will include opportunistic and usually abundant (density-successful) species within their distribution range. They are characterized by flexible diets and habitat use and little or no prey preferences across ecosystems. Species-specific ontogeny sets a range of exploitable resources in Ubi consumers (mainly through the ontogeny of the feeding apparatus) however trophic and cross-habitat foraging are essentially determined by ecosystem features affecting resources availability. This was the case for both Brook Trout and White Sucker, based on our observations but also on literature evidence of the variable and opportunistic character of their feeding ecology. Frequent habitat and diet switches in response to varying prey densities or factors affecting prey densities (i.e. inter-specific interactions) are common in Ubi consumers and are independent of their ontogeny. As a result, this consumer type is characterized by highly variable bi-dimensional resource use between ecosystems.

The Aequivocus type includes consumers who tend to be more specialized in their habitat and dietary choices, as per their ontogeny. This specialization is in turn responsible for a marked sensitivity to resource exploitation under community interactions. The Aequivocous type was represented by Long Nose Sucker in our study lakes. Life-stage and among-lake patterns of bi-dimensional resource use in Long Nose Sucker demonstrated the strength of life-history effects on horizontal foraging and trophic positioning in this consumer type. It also showed the influence of physical ecosystem structure and community composition and interactions in determining trophic omnivory and inter-habitat resource use and feeding diversity in Aequicovus consumers. Contrary to Ubi consumers, inter-specific interactions do not yield transient diet switches in

Aequivocus species, but directly interfere with their life-history strategies. Consequently, bi-dimensional resource use in Aequivocus consumers will tend to be relatively constant between ecosystems with similar community composition, but variable between biogeographic regions and associated differences in species composition and physical ecosystem structure.

Table 1-7. Summary of autecological types general traits.

	QUIS TYPE	UBI TYPE	AEQUIVOCUS TYPE
General traits - Ontogeny	Rigid metabolic requirements for prey and habitat selection in adult stages	Flexibility of resource exploitation only limited by the ontogeny of the feeding apparatus	Characterized –but not limited by – ontogenetic prey and habitat preferences
Resource exploitation	Definite ontogenetic habitat and dietary shifts across ecosystems	Frequent and transient dietary-habitat switches in response to variations in resource availability and profitability	Ontogenetic habitat and dietary shifts influenced by physical ecosystem features and community composition and interactions
Others	Sensitivity to intra-specific competition	Abundant species within their distribution range	marked sensitivity to community interactions

Table 1-7 summarizes the key features of each autecological type. Bi-dimensional feeding ecologies classified by autecological type recognize the functional role of consumers as partly (Quis and Aequivocus types) or mainly (Ubi type) defined by the characteristics of their environment. From this we can formulate hypothesis regarding consumer flexibility in bi-dimensional resource use in the context of environmental variability. "Flexibility" in this case allows for changes in spatially explicit resource use with little or no alteration to population structure. Based on this, Ubi consumers can be expected to demonstrate great

flexibility in both vertical and horizontal resource use, since their feeding ecology is only limited by an array of exploitable resources determined by their feeding morphology (Fig.1-8). Thus Ubi consumers will easily adapt to changing environmental conditions via changes in trophic and cross-habitat foraging unlikely to affect their population structure in the short term. In contrast, a limited flexibility in vertical and horizontal resource use can be expected in Quis consumers, due to ontogenetically-defined metabolic limitations on prey selection (Fig. 1-8).

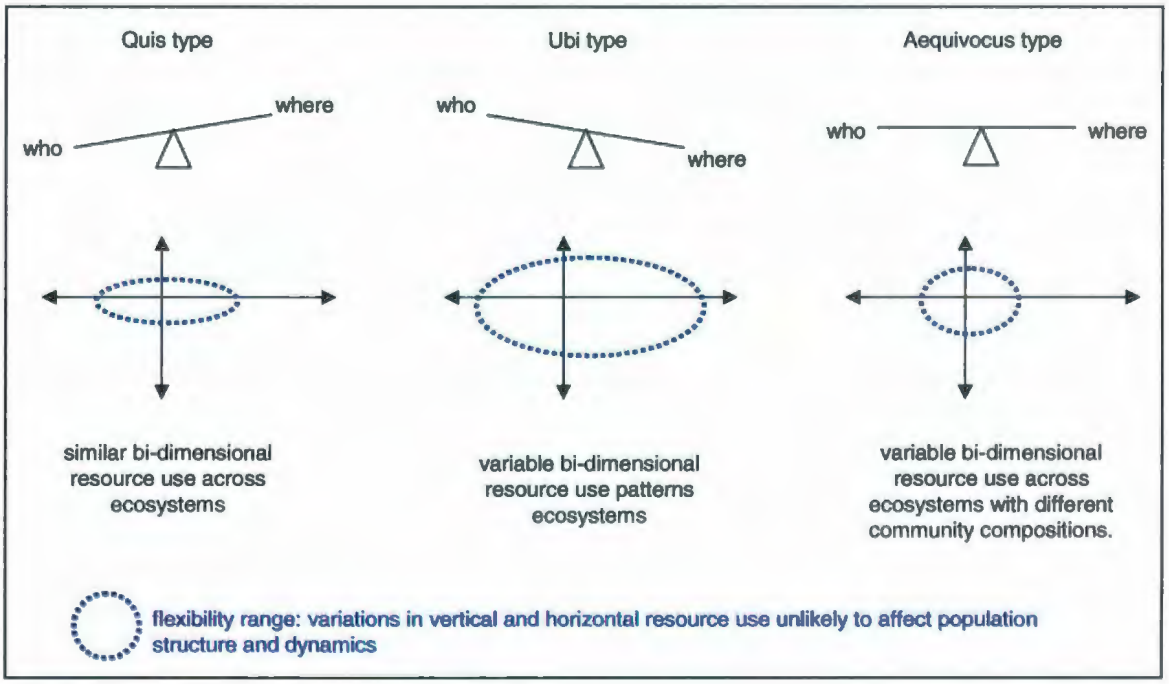

Fig. 1-8. The balance between species specific (of "who" consumers are) and ecosystem specific influences (or "where" consumers live) that distinguish consumer bi-dimensional feeding strategies into three autecological types, also delineate consumer flexibility in bi-dimensional resource use among ecosystems or in response to changing ecosystem conditions (flexibility range).

To a certain extent, Quis consumers will adapt to perturbations affecting prey availability via changes in horizontal resource use. Changes in preferred habitat structure affecting

prey density, foraging efficiencies and intra-specific interactions however, will rapidly have detrimental effects on Quis consumer population structure. In Aequivocus consumers, a greater specialization and sensitivity to community interactions can be expected to confer an intermediate flexibility in vertical and horizontal resource use. Aequivocus species will be most vulnerable to habitat disruption or changes in community composition affecting optimal prey and habitat utilization. However depending on physical ecosystem attributes, Aequivocus consumers may be more resilient than Quis consumers and able to overcome population consequences via life-stage specific changes in two-dimensional prey and habitat use.

CONCLUSION

A bi-dimensional approach to feeding ecology provides a simple conceptual framework by which to distinguish the functional role and flexibility of consumer species in two-dimensional space of ecosystems. Viewed together, vertical and horizontal resource utilization offer new perspectives into the interplay of feeding relationships and ecosystem attributes. Our comparative analysis has shown how ecosystem characteristics determine horizontal resource use and feeding diversity in consumers, affect the extent of vertical energy flows, and modulate the intensity of intra and inter-specific interactions, depending on species. Further investigations are now required to validate the application of bi-dimensional resource use theory on different consumer and ecosystem types. We believe this approach constitutes a scale-independent framework permitting the integration of spatial influences on consumer populations wherever spatially distinct carbon sources can be identified and traced through food webs, and where basic

information on consumer biology is available. Knowledge of consumer bi-dimensional feeding ecologies and autecological types, may serve as practical means of evaluating species sensitivity to disturbance for management or conservation purposes, and further to untangle complex environmental issues like contaminant bioaccumulation and cycling.

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2. Chapter 2

FROM BI-DIMENSIONAL FEEDING ECOLOGIES TO BI-DIMENSIONAL FOOD WEB STRUCTURE

ABSTRACT

Horizontal (spatially-explicit) and vertical (trophic) energy flows can be integrated into a bi-dimensional framework to provide more explicit understanding of the ecology of consumer species. We have shown that consumer bi-dimensional feeding ecologies are determined by species ontogeny and ecosystem characteristics. Based on this, consumers can be classified in autecological types that may serve to evaluate species response to change or perturbations in their environment. Here we take the bi-dimensional approach to the food web level. Using data from the entire fish communities of the former study lakes, we demonstrate how bi-dimensional food web structure can be estimated from average vertical (trophic) and horizontal (cross-habitat) resource use in consumer communities, each quantified by variations in stable isotope ratios of nitrogen and carbon, respectively. Horizontal resource use here corresponds to the coupling of littoral-pelagic carbon source by fish communities in lakes. This comparative analysis permits us to link vertical trophic organization with ecosystem productivity, community composition and horizontal energy flows determined by spatial patterns in ecosystem structure. We show that differences in bi-dimensional food web structure among ecosystems provide alternative stable states for communities, depending on primary productivity constraints at the food web base and the physical extent of spatially distinct habitats. On a system-to-system basis, we suggest that cumulative autecological types in consumers will determine flexibility in bi-dimensional food web structure. A bi-dimensional approach thus improves our understanding of the ecological processes that underlie community organization and resilience. As such, it may serve as a solid conceptual basis to address local and global anthropogenic impacts on biological communities.

INTRODUCTION

Human activities are impacting natural systems to an unprecedented degree, causing regional and global environmental perturbations affecting physical and biological components of ecosystems. Physical alterations of natural environments first cause changes in the spatial distribution and feeding patterns of living organisms, prior to altering population and community integrity. Feeding strategies affect community composition (Naiman 1988) and community structure determines the flow of energy, nutrients, and contaminants through ecosystems (Hebert et al. 2006). Thus on a system to system basis, changes in food web structure can be a good indicator of variations in ecosystem condition. Understanding food web structure and the ecological processes that underlie community organization can improve our comprehension of anthropogenic impacts on natural systems and facilitate the formulation of appropriate prevention measures and mitigation efforts.

Food web structure and spatial considerations

Food web structure is a leading concept in food web ecology that relates food web patterns with the dynamic processes that modulate them (Pimm 1982, Morin and Lawler 1995). Pioneer work by Lindeman (1942) depicted energy sources and flows together as foundations for food web architecture and dynamics. Yet subsequent developments in food web research have been essentially linear and unidimensional, focusing on "who eats whom" and on the direction and strength of interactions (i.e. trophic cascade) with little consideration of spatial dynamics and habitat utilization or "who eats whom and where". As a result, food web structure has been distilled to its vertical, trophic dimension. More recently, consequences of anthropogenic pressures on the environment

have challenged conventional simplifications of complex and adaptive natural systems. Environmental disturbances have imposed the relationship between complexity and sustainability as an emergent ecosystem property. This was paralleled by the resurgence of spatial and landscape considerations in general ecology and food web principles (Turner 1989, Dunning et al. 1992, Polis et al. 1997, Tilman and Kareiva 1997, Huxel and McCann 1998, Holt 2002, Polis et al. 2004, Lovett et al. 2005). Spatial linkages across variable spatial-scales (i.e. between ecosystems in a landscape or between habitats within an ecosystem) are now recognized as key delineators of ecosystem processes (Lundberg and Moberg 2003, Turner 2005). Spatial influences on ecological systems can be partitioned as spatial patterns and spatial processes. Spatial patterns refer to among and within-ecosystems variability in biological and physical structure, including spatial heterogeneity, complexity, dimensionality, and landscape composition and physiognomy. Spatial processes are interactions, linkages, or fluxes between spatially distinct ecosystems or habitats. At the food web level, spatial patterns provide for distinct carbon sources that can be coupled via spatially explicit foraging in consumers, a fundamental spatial process in food web ecology. Spatial patterns also stabilize community interactions by providing refuges (Connell 1972, Luckinbill 1974, Sass et al. 2006), by sustaining alternative prey for consumers between spatially distinct ecosystems or habitats (Holt 1984) and by regulating consumer foraging success and yields (Diehl 1988, Whitehead and Walde 1992). As a result, trophic structure and interactions are linked to spatial processes determined by the spatial context of community architecture (Fig. 2-1).

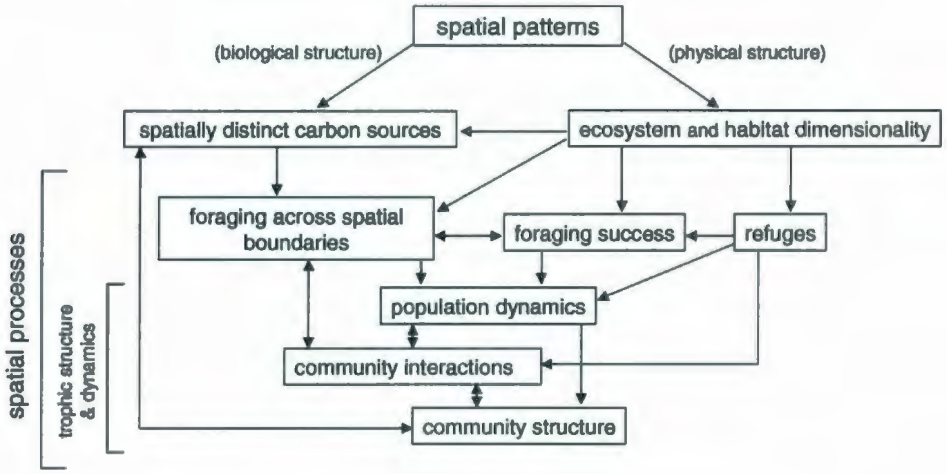

Fig. 2-1. Scale-independent spatial influences for food webs.

Bi-dimensional food web structure

Recognizing the intrinsic character of spatial patterns and processes for community organization and dynamics, we propose to reintegrate spatially distinct energy sources-pathways in the conceptualization of food webs. Bi-dimensional food web structure relates horizontal spatial processes to vertical trophic organization. Horizontal spatial processes here involve spatially distinct primary producer-consumer population dynamics and ensuing spatial fluxes and/or subsidies in secondary and tertiary consumers. A bi-dimensional approach to food web structure thereby relates energy sources and energy flows on two orthogonal, mobile axes (Fig. 2-2). Axes intersection (i.e. the position of the vertical axis relative to the horizontal axis) quantifies the proportion to which spatially distinct carbon sources contribute to trophic structure and interactions at the consumer level. As species ontogeny and ecosystem features determine bi-dimensional feeding strategies in consumers (Chapter 1), we expect that bi-dimensional food web structure

will vary with spatial patterns in ecosystem features and consumer community composition.

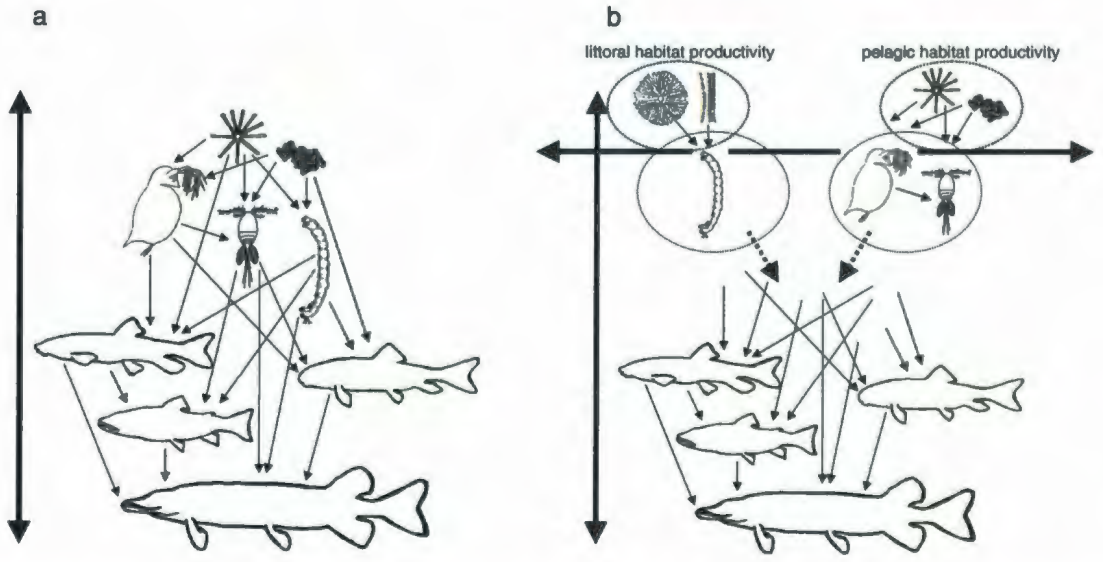

Fig. 2-2. Simplified lake food web structures. (a) Traditionally one-dimensional (vertical) food web structure depicting trophic organization or « who eats whom » and the direction of energy flows. (b) Bi-dimensional food web structure integrating horizontal spatial processes as contributions from spatially distinct carbon sources to trophic organisation and interactions at the consumer level. The position of the vertical axis relative to the horizontal axis indicates the proportion to which spatially discrete carbon sources (located on either end of the horizontal axis) contribute to vertical energy flows (here corresponding to a littoral-based food web).

In this chapter, we extend our comparative stable isotope analysis of bi-dimensional feeding strategies in fish consumers (in Chapter 1) to the entire fish communities of lake ecosystems. This study will (i) demonstrate how bi-dimensional food web structures can be estimated from average vertical and horizontal resource use in consumer communities, (ii) examine the factors that may explain differences in bi-dimensional food web structure among ecosystems, and (iii) discuss how changes in bi-dimensional food web structure may relate to community resilience and stability.

METHODOLOGY

Methods used for sample collection, study lake characterization and stable isotope measurements are detailed in Chapter 1. Stable isotope ratios of nitrogen and carbon were used to determine individual fish trophic position (vertical resource use) and reliance upon littoral-pelagic carbon sources (horizontal resource use) in lakes, respectively. For each lake, bi-dimensional food web structure was estimated as the sum of fish consumer trophic position and littoral-pelagic resource use weighted by species and size class (Fig. 2-3). Four different fish species were sampled in each lake and three different size classes were a priori defined in each species (see Chapter 1).

VERTICAL food web structure =

species 1 species 2 species 3 species 4

$$((\Sigma TrophP_1/n_1^{sc})/(n^i/n^s)) + ((\Sigma\ TrophP_2/n_2^{sc})/(n^i/n^s)) + ((\Sigma\ TrophP_3/n_3^{sc})/(n^i/n^s)) + ((\Sigma\ TrophP_4/n_4^{sc})/(n^i/n^s))$$

HORIZONTAL food web structure =

specie 1 specie 2 specie 3 specie 4

$$((\Sigma\%C_{LITT/PEL1}/n_1^{sc})/(n^i/n^s)) + ((\Sigma\%C_{LITT/PEL2}/n_2^{sc})/(n^i/n^s)) + ((\Sigma\%C_{LITT/PEL3}/n_3^{sc})/(n^i/n^s)) + ((\Sigma\%C_{LITT/PEL4}/n_4^{sc})/(n^i/n^s))$$

Where:

	TrophP	= individual fish consumer trophic position
	$\%C_{LITT/PEL}$	= individual fish consumer percent reliance on littoral versus pelagic carbon sources
	n^{sc}	= number of size classes per species (=3)
	n^i	= total number of fish sampled in a lake
	n^s	= number of different species sampled in a lake (=4)

Fig. 2-3. Calculations for lake-specific estimations of vertical and horizontal food web structure.

This approach accounts for differences in sample numbers by species, size class and lake. Estimates of vertical food web structure are used to compare the extent of vertical energy flows among lakes (i.e. food chain length). Estimates of horizontal food web structure are used to compare the relative contributions of littoral versus pelagic carbon source to lake food webs. Community averages of vertical trophic position and horizontal littoral-

pelagic resource use were also compared statistically. Differences in means were compared using the Kruskal-Wallis one-way analysis of variance since not all residuals assumptions were met (i.e. variances differed among lakes). Variances were compared using Levenes' test and used as indicators of community trophic omnivory (variability around mean estimates of trophic position) and littoral-pelagic feeding diversity (variability around mean estimates of horizontal littoral-pelagic resource use). All statistical analysis were conducted on SYSTAT software.

RESULTS

Table 2-1 shows physical and biological characteristics of the study lakes, together with the main biological features of fish communities considered for analysis.

On average, fish from Enakapeshakamau Lake were smaller relative to other fish communities and younger than fish from Ashuapamatikuan Lake. This reflects the abundance of smaller-size Brook Trout (Salvelinus fontinalis) in the Enakapeshakamau sample (see Chapter 1). The Enakapeshakamau fish community was characterized by a lower mean trophic position and greater reliance on littoral carbon. This was supported by lower and higher estimates of vertical and horizontal food web structure, respectively. Trophic omnivory was also reduced in Enakapeshakamau relative to other lakes. The bi-dimensional food web structure of Enakapeshakamau lake thus exhibited a shorter food chain primarily sustained by littoral carbon sources (Fig. 2-4b). Enakapeshakamau was characterized by a larger perimeter to area ratio. At the time of sampling, littoral and pelagic primary productivity were low in Enakapeshakamau lake.

Table 2-1. Characteristics of lake ecosystems and fish communities considered for analysis, with among-lake differences in mean fork length (FL), Age, trophic position (TrophP), percent reliance on littoral-pelagic carbon ($\%C_{LITT/PEL}$) and variance comparisons (W statistics) (for community estimates of TrophP and $\%C_{LITT/PEL}$). Estimates of vertical and horizontal food web structure weighted by species and size class (see Fig. 2-3) are also reported.

	Ashuapamatikuan	**Enakapeshakamau**	**Mistashini**	**Papauakamau**		
Surface Area (km^2)	17.21	20.65	6.21	27.43		
Drainage Area (km^2)	3433	1240	277	323		
Perimeter/ Area ratio	1.61	2.64	1.64	1.60		
Z_{max} (m)	115	26	2	20		
Chla(pel) ($\mu g\ L^{-1}$)	0.67	0.82	1.94	2.68		
Biomass(peri) ($\mu g/cm^2$)	1492	610	2464	1567		
%Chla(peri)	1.82	0.39	1.81	1.95		
Fish community composition	LNS, LT, NP, WF	BT, LNS, NP, WS	BT, LNS, NP, WS	BT, LNS, NP, WS		
n	73	68	64	36	statistic	p-value
Mean FL (mm) (±SD)	443 ± 218	305 ± 135	435 ± 213	460 ± 223	$F_{3,237}$=8.19	p<0.001
FL-range	67-840	84-732	65-985	70-930		
Mean Age (±SD)	14 ± 9	8 ± 6	10 ± 7	11 ± 6	$F_{3,212}$=6.12	p=0.001
Age-range	1-38	1-27	0-29	1-20		
Mean TrophP (±SD)	3.1 ± 0.5	2.5 ± 0.2	2.9 ± 0.4	3.3 ± 0.4	$H_{3,237}$=100.70	p<0.001
TrophP-range	2.3-4.0	2.2-3.2	2.1-3.7	2.6-4.0	$W_{n=241}$=17.27	p<0.001
estimate of Vertical food web structure	**3.94**	**3.31**	**3.85**	**4.36**		
Mean $\%C_{LITT/PEL}$ (±SD)	26 ± 31	62 ± 16	35 ± 13	40 ± 13	$H_{3,237}$=85.75	p<0.001
$\%C_{LITT/PEL}$-range	0-100	12-91	9-71	11-70	$W_{n=241}$=13.81	p<0.001
estimate of Horizontal food web structure	**34.82**	**82.15**	**46.77**	**53.04**		

Legend: Z_{max}=maximum depth, Chla(pel)=pelagic chlorophyll-a concentrations, Biomass(peri)=periphyton biomass, %Chla(peri)= periphyton percent chlorophyll-a relative to periphyton biomass. BT=Brook Trout (Salvelinus fontinalis), LNS=Long Nose Sucker (Catostomus catostomus), LT=Lake Trout (Salvelinus namaycush), NP=Northern Pike (Esox lucius), WF=White Fish (Coregonus clupeaformis), WS=White Sucker (Catostomus commersoni). n=total number of fish sampled in each lake. Range=minimum-maximum values.

In Papauakamau Lake, the fish community was characterized by a greater mean trophic position and a higher estimate of vertical food web structure. The bi-dimensional food web structure of Papauakamau lake exhibited a longer food chain sustained by almost equivalent littoral and pelagic carbon source contributions (Fig. 2-4d). Papauakamau has the largest surface area and was the most productive (in terms of both pelagic and littoral primary productivity) at the time of sampling.

In Mistashini Lake, the fish community had intermediate trophic position and littoral-pelagic resource use values. Its bi-dimensional food web structure was characterized by an intermediate food chain length sustained by almost equivalent littoral and pelagic carbon source contributions, similar to Papauakamau lake (Fig. 2-4c). Mistashini was physically distinct from other lakes in being smaller and shallower. Its rocky shores were characterized by important periphyton biomass mostly consisting in filamentous green algae (field observations).

Ashuapamatikuan Lake had a different fish community composition characterized by the absence of Brook Trout (*S. fontinalis*) and White Sucker (*Catostomus commersoni*) and the presence of Lake Trout (*Salvelinus namaycush*) and White Fish (*Coregonus clupeaformis*). Lower mean reliance on littoral carbon sources and a lower estimate of horizontal food web structure characterized this fish community. Littoral-pelagic (or littoral-profundal benthic) feeding diversity was greater in Ashuapamatikuan fish. The bi-dimensional food web structure of Ashuapamatikuan lake demonstrated an intermediate food chain length similar to that observed in Mistashini lake, however primarily supported by pelagic carbon sources (Fig. 2-4a). Ashuapamatikuan was a very deep oligotrophic lake with a larger drainage area. At the time of sampling, the lake was

characterized by very low pelagic primary productivity and intermediate littoral periphyton productivity.

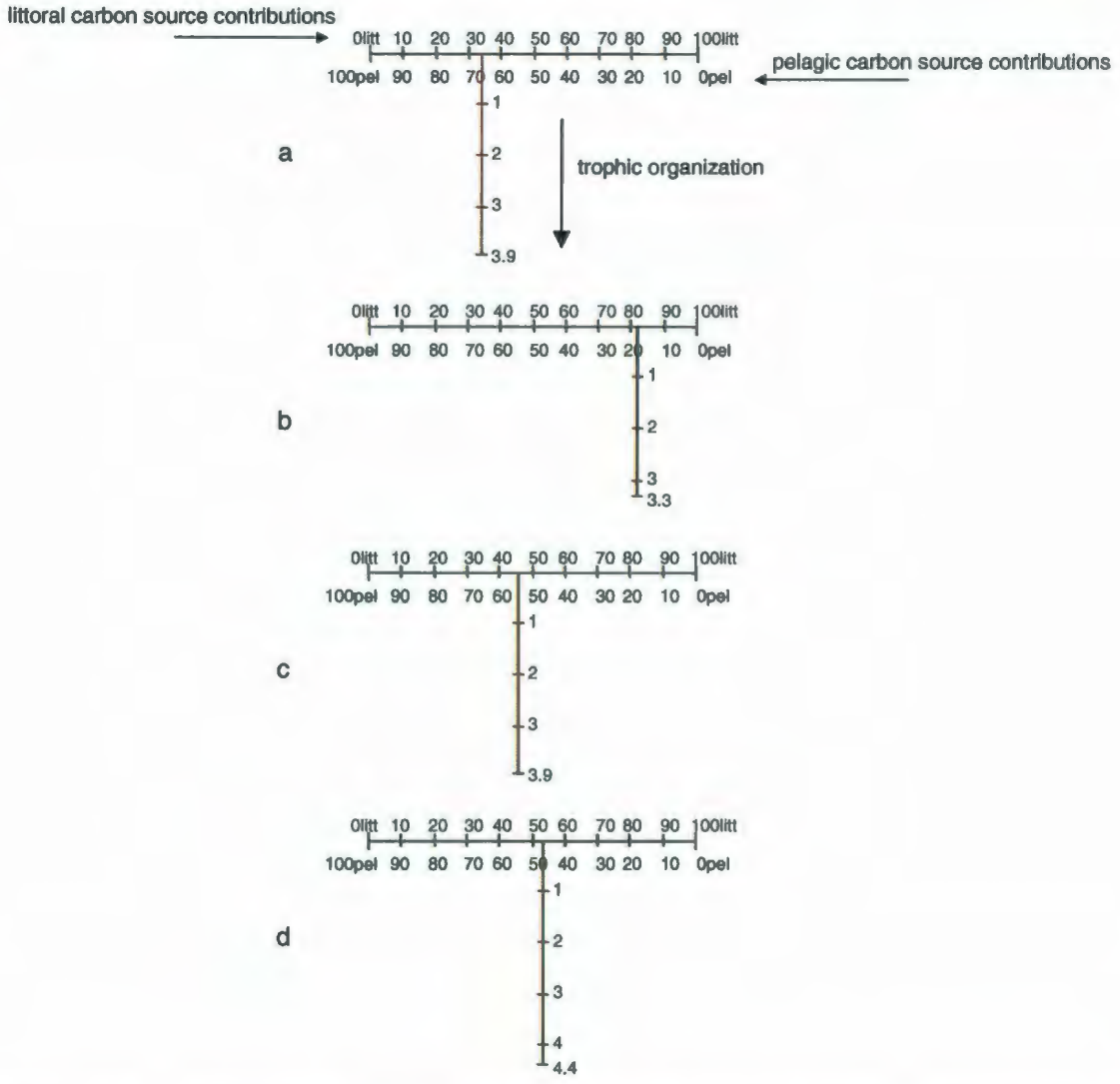

Fig. 2-4. Bi-dimensional food web structures of (a) Ashuapamatikuan lake, (b) Enakapeshakamau lake, (c) Mistashini lake and (d) Papauakamau lake. In each lake, vertical and horizontal axes values were determined by the sum of fish consumers trophic position and littoral-pelagic resource use weighted by species and size class, respectively (see equations in Fig. 2-3).

In each lake, vertical trophic organization was linked to either dominant-pelagic (>50%) or dominant-littoral (>50%) carbon source contributions at the level of fish consumers. Neither carbon source totally dominated (i.e. contributed 100%) or did not contribute to vertical energy flows. Littoral-pelagic contributions were closer to equality (50%) in Mistashini and Papauakamau lakes (Fig. 2-4c and 2-4d). In contrast, the bi-dimensional food web structures of Ashuapamatikuan and Enakapeshakamau lakes were clearly asymmetric, with dominant pelagic and littoral contributions, respectively (Fig. 2-4a and 2-4b). Lake-specific estimates of vertical and horizontal food web structure did not significantly correlate to any lake characteristics, due to our small lake sample number. All fish considered, vertical trophic position was negatively correlated to littoral-pelagic resource use across the study lakes ($n=241$, $r=-0.304$, $p<0.001$).

DISCUSSION

Bi-dimensional food web structures differed with community composition (i.e. in Ashuapamatikuan relative to other lakes) and among lakes with similar fish communities (i.e. in Enakapeshakamau relative to Mistashini and Papauakamau lakes). Ashuapamatikuan and Enakapeshakamau lakes had asymmetric bi-dimensional food web structures exhibiting dominant pelagic or littoral carbon source contributions to vertical energy flows. Such asymmetry is consistent with past (Darnell 1961) and more recent (Polis and Strong 1996, Huxel and McCann 1998, Holt 2002, Vadeboncoeur et al. 2005, Rooney et al 2006) suggestions that spatial processes as uneven contributions from spatially distinct carbon sources, may be a general feature and important stabilizing mechanism for food webs. These assertions usually rely on the principle that spatial

boundaries allow asynchronous population dynamics to occur at lower (primary producer-consumer) trophic levels. This provides secondary and tertiary consumers with more stable prey resources on ecosystem-scale, thereby stabilizing consumer populations and entire food webs. In our study lakes, asymmetry was concurrent to lower primary productivity at the food web base. Hence Ashuapamatikuan and Enakapeshakamau were the most oligotrophic of the study lakes. In contrast, the two lakes characterized by greater planktonic and periphyton primary productivity exhibited almost equivalent littoral and pelagic contributions to vertical energy flows.

Comparable littoral-pelagic contributions supported a longer food chain in the larger and more productive Papauakamau lake. A longer food chain was expected with both ecosystem size and productivity hypotheses for this lake (Vander Zanden et al. 1999, Post 2002b). It may also be related to important littoral-pelagic habitat coupling at the level of fish consumers. In contrast, the shorter food chain of Enakapeshakamau lake was linked to dominant littoral carbon contributions to vertical energy flows. This pattern was mainly responsible for the negative correlation between fish trophic position and littoral-pelagic resource use in the study lakes. Dominant littoral resource use by fish consumers in Enakapeshakamau was related to its larger perimeter to area ratio (see species-specific correlations in Chapter 1). This physical characteristic likely contributed to broaden the "effective dimensionality" of community dynamics in this lake (Holt 2002). Dimensionality favors the spatial aggregation of aquatic consumer communities (Scheuerell and Schindler 2004, Sass et al. 2006). It also positively influences foraging success in top predators (Whitehead and Walde 1992). In consequence, habitat dimensionality affects population viability and bi-dimensional food web structure. In

Enakapeshakamau lake, dominant littoral spatial processes permitted by greater littoral habitat dimensionality may have worked to stabilize community structure in the context of low primary productivity (Holt 2002, Rooney et al. 2006). The resulting bi-dimensional food web structure sustains a fish community similar to that of Papauakamau and Mistashini lakes, despite natural constraints on resource availability. Comparatively reduced trophic omnivory in Enakapeshakamau consumers supports this contention. Hence spatial aggregation within the littoral habitat likely intensified inter- and intra-specific interactions in this lake, forcing consumer species to narrow the trophic range of their diets. Alternatively, reduced trophic omnivory may be a direct response to resource limitation (low productivity) and/or the consequence of physical attributes (such as a large perimeter to area ratio) providing access to particular, more energetically favorable prey. Selective foraging on such prey, at the expense of trophic omnivory, may also function to maintain food web stability (Post et al. 2000a). A shorter food chain in Enakapeshakamau lake was thus related to primary productivity constraints at the food web base and to limited littoral-pelagic habitat coupling permitted by the physical extent of the littoral habitat. Physical ecosystem structure similarly explained the bi-dimensional food web configuration of Ashuapamatikuan lake. This lake was characterized by great depth and extensive pelagic and profundal-benthic habitats. This supported an alternative fish community composition characterized by the presence of a pelagic top-predator (*S. namaycush*) and a benthic-pelagic forage fish (*C. clupeaformis*). A different community composition and physically extensive pelagic/profundal-benthic habitats explained that vertical energy flows were primarily sustained by pelagic spatial processes in Ashuapamatikuan lake, despite very low pelagic primary productivity. Pelagic

contributions in this case probably included profundal-benthic carbon sources, since the two signatures are isotopically similar (Vander Zanden and Rasmussen 1999). The resulting bi-dimensional food web structure of Ashuapamatikuan lake supported a food chain length comparable to that observed in the more productive Mistashini lake. This suggests that the extent of vertical energy flows was related to physical ecosystem structure, consumer community composition and littoral-pelagic and profundal-benthic habitat coupling in this lake. Greater littoral-pelagic feeding diversity in the Ashuapamatikuan community indicated that littoral dietary pathways still played a key role in maintaining consumer production and stability in this food web. Littoral contributions were supported by relatively important periphyton productivity in the littoral habitat of Ashuapamatikuan lake.

These observations indicate that food chain length was a consequence of interacting constraints imposed by ecosystem and habitat dimensionality, productivity and food web stability in the study lakes. This has been partly suggested by Briand and Cohen (1987), Persson et al. (1992), and Post (2002b). Food web stability in this case was imparted by differing contributions of spatially distinct carbon sources to vertical energy flows, or alternate bi-dimensional food web structures. Differences in bi-dimensional food web structure among lakes were linked to spatial patterns in physical and biological ecosystem characteristics and consumer community composition. Lower primary productivity was related to asymmetry in bi-dimensional food web structure, as was the greater physical extent and dimensionality of one habitat relative to another. Our comparative analysis demonstrated how vertical trophic organization is related to ecosystem and inter-habitat productivity, to consumer community composition, and to horizontal spatial processes

determined by spatial patterns in ecosystem structure. This confirms that horizontal spatial processes, together with vertical energy flows, are complementary basis for food web structure. It also emphasizes changes in bi-dimensional food web structure as an important stability mechanism for food webs.

FURTHER IMPLICATIONS

Differences in bi-dimensional food web structure among ecosystems are related to physical and biological ecosystem characteristics. For a particular system however, changes in bi-dimensional food web structure are likely related to a balance between community composition and ecosystem effects, similar to that observed at the consumer level. In consumers, the balance between species and ecosystem influences determined bi-dimensional feeding strategies with varying flexibility, which we proposed to classify under Autecological types (Quis, Ubi and Aequivocus) (Chapter 1). At the community level, we suggest that community composition similarly determines flexibility in bi-dimensional food web structure. In this perspective, community composition corresponds to the sum of individual consumer species' autecological types. Figure 2-5 illustrates this concept as it applies to our study lakes. Cumulative autecological types in Enakapeshakamau, Mistashini and Papauakamau lakes yield Ubi-dominant communities (Fig. 2-5A). Like Ubi consumers, we expect that trophic and spatial processes in Ubi communities are mainly determined by ecosystem features. In consequence, Ubi communities should have flexible bi-dimensional food web structures. Changing ecosystem conditions causing changes in trophic and spatially-explicit resource use therefore, are unlikely to alter population structure and community integrity in Ubi-

dominant food webs. In Ashuapamatikuan lake, cumulative autecological types instead correspond to a Quis-dominant community (Fig. 2-4B). Like Quis consumers, we expect that trophic and spatial processes in Quis communities are constrained by consumer life-history strategies. In consequence, Quis communities should have relatively rigid bi-dimensional food web structures. Changes in trophic and spatially-explicit resource use in response to environmental fluctuations will directly interfere with consumer life-history traits in Quis communities. This will alter population structure and eventually cause changes in species composition (initially by the loss of demanding autecological types like Quis consumers).

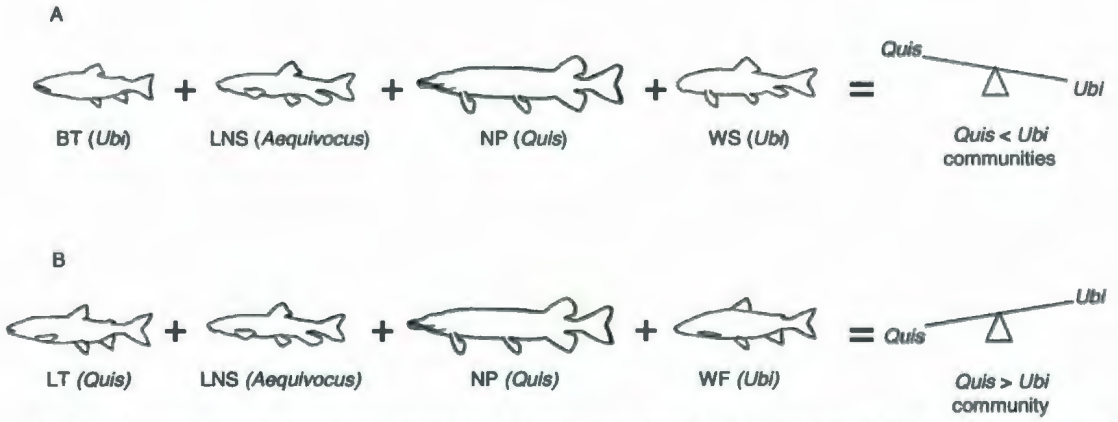

Fig. 2-5. Cumulative autecological types for fish communities of (A) Enakapeshakamau, Mistashini and Papauakamau Lakes and (B) Ashuapamatikuan Lake.

An intermediate community type would be dominated by Aequivocus consumers and exhibit an intermediate flexibility in bi-dimensional food web structure.

Viewed as such, flexibility in bi-dimensional food web structure for a particular system relates to community resilience. The amount of disturbance required to induce a change in community composition will be greater in ecosystems characterized by Ubi and

Aequivocus relative to Quis communities. This is if we expect environmental constraints to be mediated by compensatory spatial-trophic foraging leading to changes in bi-dimensional food web structure.

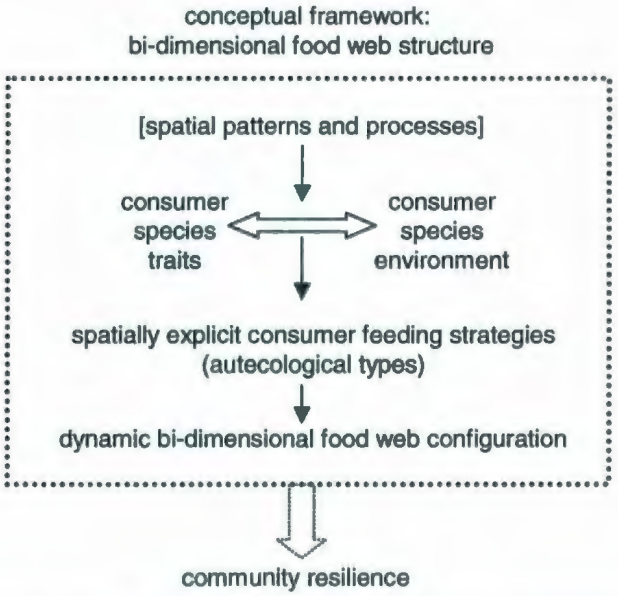

Fig. 2-6. Bi-dimensional food web structure as a conceptual framework integrating the influences of spatial patterns and spatial processes for food webs: overall implications.

A bi-dimensional approach may thus reduce the importance of defining specific thresholds for numerous and complex environmental parameters (which is a common difficulty in ecological management (Groffman et al. 2006)), by alternatively focusing on community sensitivity to environmental fluctuations, as outlined in two-dimensional space of ecosystems (Fig. 2-6). By extension, we can speculate that fluctuating or perturbed environments will favor the establishment and persistence of Ubi (or Aequivocus) communities within a landscape, while Quis communities will be characteristic of relatively stable environments. Further work is now required to evaluate

temporal changes in ecosystem-specific bi-dimensional food web structures, and to validate this community resilience hypothesis.

CONCLUSION

Bi-dimensional food web structure is a conceptual framework that integrates spatial patterns and processes in community architecture. Our demonstration of this approach on natural lake communities has shown the ease of application and ecological relevance of estimates of bi-dimensional food web structure based on stable isotope quantifications of vertical and horizontal resource use in consumers. The proportions to which spatially distinct carbon sources contribute to vertical energy flows, is a system-specific feature determined by the physical and biological characteristics of ecosystems and consumer community composition. Differences in bi-dimensional food web structure among ecosystems thereby demonstrate alternative stable states for communities. On temporal scales, this approach may serve to further our understanding of the mechanisms by which communities adapt to environmental change. Thus wherever spatially-distinct carbon sources can be identified and traced through food webs, a bi-dimensional approach will provide a solid conceptual basis for spatially-explicit ecological understanding and modeling. We believe that bi-dimensional food web structure can serve to improve ecosystem, habitat and species conservation and management strategies in the face of growing anthropogenic perturbations of natural systems and global environmental change.

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----- SECOND MOVEMENT:

Bi-dimensional feeding strategies and food web structure, Application to Hg bioaccumulation in fish

3. Chapter 3

Bi-Dimensional Feeding Strategies link Species and Ecosystem Determinants of Mercury Bioaccumulation in Fish

ABSTRACT

Fish consumption is the main pathway for mercury (Hg) exposure in human populations. Several factors have been identified to explain differences in Hg bioaccumulation in fish, but their effects remain independent from one another and at best valid in localized areas. Hg pollution management remains complicated by spatial variations in fish Hg levels among ecosystems receiving comparable Hg inputs. Bi-dimensional or spatially-explicit feeding ecologies link the vertical (trophic) and horizontal (cross-habitat) energy flows that together support consumer production. Autecological types classify consumers bi-dimensional resource exploitation as shaped mainly by consumer ontogeny (Quis type), by ecosystem characteristics (Ubi type) or both (Aequivocus type). Bi-dimensional resource use by fish consumers integrates spatial influences on Hg exposure and trophic transfers in two-dimensional space of aquatic systems. Thus we suggest that bi-dimensional feeding ecologies classified by autecological type may serve to relate species and ecosystem determinants of Hg bioaccumulation in fish. We characterized bi-dimensional resource use in three fish species each representing an autecological type across four pristine lake ecosystems using stable isotope ratios of nitrogen and carbon. Based on this, we (i) confirm that horizontal (littoral-pelagic) foraging modulates Hg exposure and uptake for fish species within and among lake ecosystems, and (ii) demonstrate that autecological type determines the influence of species versus ecosystem characteristics on Hg bioaccumulation in fish, and allow the identification of the factors that will likely cause spatial variations in Hg uptake on species-specific basis. Quantifying bi-dimensional feeding patterns in fish and classifying them by autecological types wherever two distinct carbon and Hg pools are available at base of food webs, facilitates the evaluation of inter-system variations in fish Hg levels by species, and may serve to improve Hg management strategies and policies to reduce human exposure.

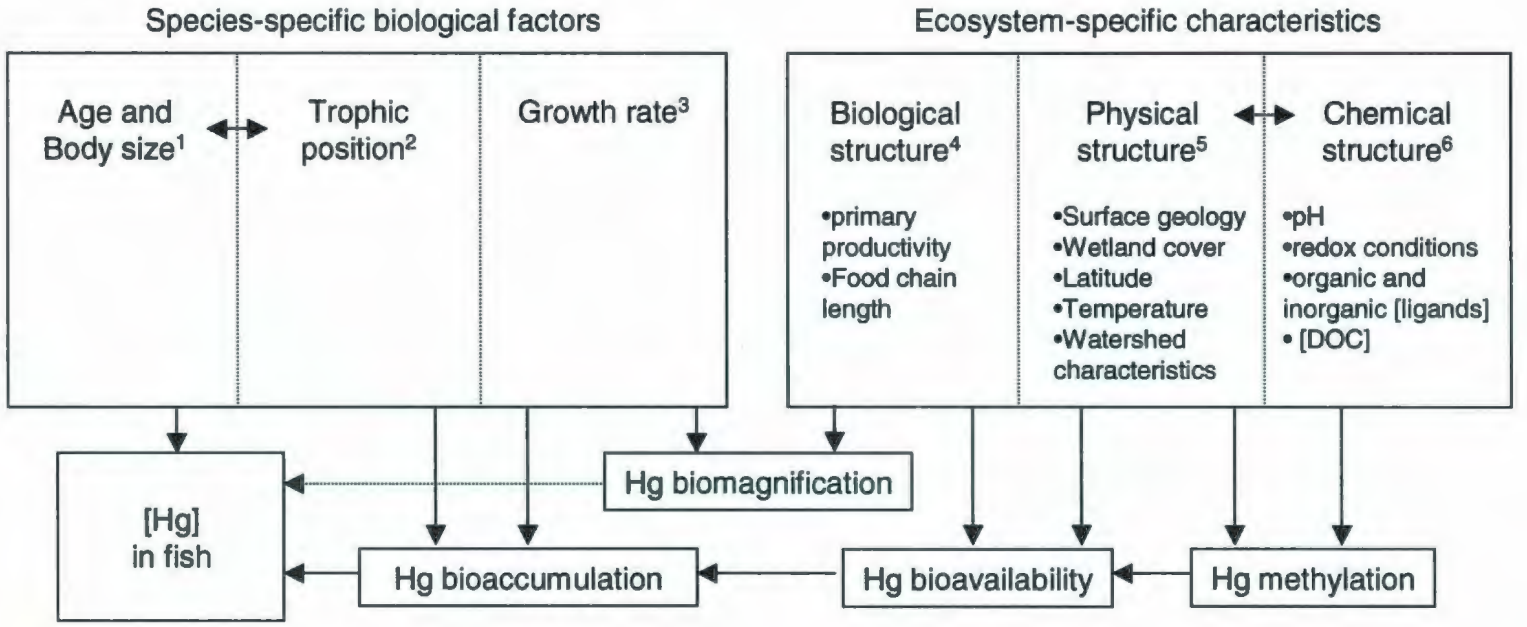
INTRODUCTION

Mercury (Hg) exposure through fish consumption remains a health concern for subsistence fishers of the Canadian boreal forest (Indian and Northern Affairs 2003, Environment Canada 2004a). Long-range atmospheric transport of anthropogenic and natural sources account for most Hg inputs to freshwater ecosystems remote from point-sources of Hg contamination (Jackson 1997, Fitzgerald et al. 1998, Wang et al. 2004). In aquatic environments, inorganic Hg is methylated into bioavailable and highly toxic methylmercury (MeHg) that can biomagnify and bioaccumulate to high levels in aquatic biota (Wiener et al. 2003). Even in lakes remote from human presence, tissue concentrations of total Hg in fish can exceed the Canadian guideline limits for safe consumption of 0.5ppm for the general population, and the recommended threshold of 0.2ppm for subsistence populations, children and pregnant women (Braune et al. 1999).

Despite an impressive number of Hg-related investigations, Hg pollution management remains complicated by spatial variations in ecosystem response to Hg loadings (Lindqvist et al. 1991, Wiener et al. 2003). This leads to variable Hg accumulation patterns and heterogeneous Hg levels in fish between ecosystems receiving comparable Hg inputs (Lindqvist et al. 1991, Schetagne et al. 1999, Indian and Northern Affairs 2003, Kamman et al. 2005). Several factors have been proposed to account for the observed inter-system and inter- and intra-specific variations in Hg levels in freshwater fish. Biological factors such as body size, growth rate, and trophic status, as well as environmental factors relating to biological, physical and chemical ecosystem structure, have been shown to affect the extent of Hg bioaccumulation (Fig. 3-1). Yet while numerous studies have identified these factors and their effects on Hg biogeochemical

pathways, biological and environmental determinants of Hg bioaccumulation in fish remain, for the most part, unconnected – and at best valid only for localized areas. This constitutes an important gap that continues to impede our ability to predict Hg concentrations in fish on a regional and system-specific basis.

In recent years, spatial complexity has emerged as an important facet of aquatic ecology. Within and among ecosystems, foraging across spatial boundaries or habitat coupling by mobile consumers affect population dynamics, community trophic cascades and food web stability (Huxel and McCann 1998, Holt 2002, Vadeboncoeur et al. 2005, McCann et al. 2005, Rooney et al 2006). In lake ecosystems, a spatial distinction between pelagic and littoral-benthic primary productivity provides alternative support for fish production through asynchronous primary producer-consumer population dynamics (France and Steedman 1996, Schindler et al. 1996, Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002, Karlsson and Byström 2005). Recent evidence for Hg methylation in littoral periphyton, and for the active transfer of MeHg to aquatic biota via periphyton communities (Cleckner et al. 1999, Desrosiers et al. 2006a, Desrosiers et al. 2006b) suggest a similar distinction in the regulation of bioavailable Hg at the base of littoral-benthic and pelagic habitats in lakes. Horizontal resource use across habitat boundaries together with vertical trophic positions, are thus likely to affect mercury bioaccumulation in fish (Lindqvist et al. 1991). Consideration of both trophic status and carbon source better described Hg variations in a sub-Arctic lake fish community, where lower and higher Hg concentrations characterized benthic and pelagic species, respectively (Power et al. 2002a). Similarly, Gorski et al. (2003) linked greater reliance on littoral-benthic



1 Downs et al. 1998, Indian and Northern Affairs 2003, Wiener et al. 2003, Evans et al. 2005. 2 Cabana et al. 1994, Kidd et al. 1995, Bowles et al. 2001, Evans et al. 2005. 3 MacCrimmon et al. 1983, Verta 1990, Greenfield et al. 2001, Stafford and Haines 2001, Simoneau et al. 2005. 4 Lindqvist et al. 1991, Meili 1991, Cabana and Rasmussen 1994, Jarman et al. 1996, Atwell et al. 1998, Kidd et al. 1999, Indian and Northern Affairs 2003, Chen et al. 2005. 5 Lindqvist et al. 1991, Meili 1991, Downs et al. 1998, Garcia and Carignan 2000, Porvari and Verta 2003, Evans et al. 2005, Shanley et al. 2005, Desrosiers et al. 2006a. 6 Downs et al. 1998, Watras et al. 1998, Mason et al. 2000, Sjöblom et al. 2000, Ullrich et al 2001, Wiener et al. 2003.

Fig. 3-1. Current state of knowledge for factors directly (species-specific) and indirectly (ecosystem-specific) influencing Hg bioaccumulation patterns and observed [Hg] in fish, with appropriate references[(1-8)].

relative to pelagic carbon to lower species-specific Hg concentrations in fish between proximate lake ecosystems.

Spatially explicit bi-dimensional feeding ecologies integrate horizontal (cross-habitat) and vertical (trophic) resource utilization by consumers (Fig.3-2). Bi-dimensional feeding ecologies are determined by species and ecosystem characteristics, the relative importance of which is species-specific (Chapter 1).

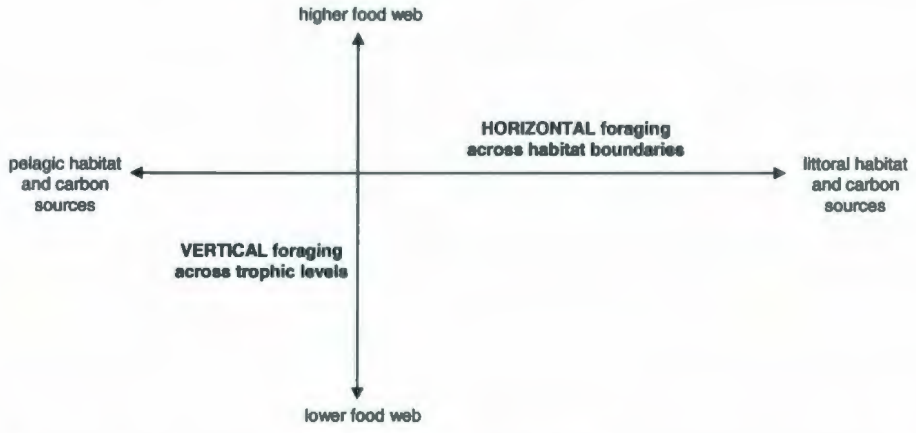


Fig. 3-2. Conceptual basis for spatially-explicit bi-dimensional feeding ecologies, as exemplified for fish consumers in lake ecosystems.

Autecological types distinguish consumer bi-dimensional feeding strategies as primarily determined by ontogeny (Quis type), by ecosystem characteristics (Ubi type) or both (Aequivocus type) (Chapter 1). This classification determines flexibility in bi-dimensional resource use among ecosystems (Table 3-1). Since dietary intake is the main pathway for Hg to fish (Hall et al. 1997), bi-dimensional feeding strategies should affect Hg exposure, transfers and uptake for fish consumers in two-dimensional space of aquatic ecosystems. Classified by autecological types, these strategies may further serve to distinguish the importance of biological (species-specific) versus environmental

(ecosystem specific) factors that determine Hg bioaccumulation in fish. Bi-dimensional feeding ecologies classified by autecological types and expected effects on Hg bioaccumulation are summarized in Table 3-1.

Table 3-1. Bi-dimensional feeding ecologies that link feeding patterns, life-history traits and ecosystem attributes, can be classified into three autecological types that distinguish spatially-explicit resource use as determined mainly by ontogeny (Quis type), by ecosystem features (Ubi type) or both (Aequivocus type). Autecological types outline inter-system variability in bi-dimensional resource use (observed) and may serve to explain spatial variations in Hg bioaccumulation in fish consumers (predicted).

		QUIS TYPE	UBI TYPE	AEQUIVOCUS TYPE
Observed (Chapter 1)	Bi-dimensional resource exploitation	determined by ontogeny	determined by ecosystem features affecting resources availability	determined by ontogeny, community composition and interactions and physical ecosystem structure
	Inter-system variability in vertical and horizontal resource use	limited	highly variable	variable between biogeographic regions and associated differences in community composition
Predicted	Dietary pathways for Hg accumulation	determined by biological factors	determined by environmental factors	determined by both biological and environmental factors
	Inter-system variability in Hg bioaccumulation	predictable	variable	predictable between ecosystems with similar community types

Bi-dimensional resource utilization determined by ontogeny in Quis-type consumers, should establish a strong influence of biological factors on Hg accumulation, making Hg concentrations predictable among ecosystems. In contrast, bi-dimensional resource use determined by ecosystem features in Ubi-type consumers, should explain highly variable dietary pathways for Hg accumulation within and among ecosystems, that will reflect spatial variations in resource availability. In Aequivocus consumers, bi-dimensional resource use equally determined by ontogeny and ecosystem features should explain a

combined influence of biological and environmental factors on Hg accumulation, and relatively predictable Hg levels among systems with similar community composition.

We used variations in stable isotope ratios of nitrogen and carbon to quantify vertical (trophic) and horizontal (cross-habitat) resource use in natural lake populations of Northern Pike (*Esox lucius* (Linnaeus)), a Quis-type consumer; White Sucker (*Catastomus commersoni* (Lacépède)), an Ubi-type consumer; and Long Nose Sucker (*Catastomus catostomus* (Forster)), an Aequivocous-type consumer. Horizontal resource utilization here distinguishes between littoral and pelagic carbon and Hg sources for fish consumers in lakes. This study aims to demonstrate that (i) bi-dimensional resource use affects Hg bioaccumulation in fish, and (ii) that species and ecosystem-specific features that determine inter-system differences in Hg levels among fish species can be assessed in the context of bi-dimensional feeding strategies classified by autecological type.

MATERIALS AND METHODS

Study Lakes

This study was undertaken as part of the Labrador component of the "Mercury in the Boreal Forest Ecosystem" research initiative, within the Canadian Collaborative Mercury Research Network (COMERN). Study lakes were selected and sampled in partnership with the Labrador Innu, based on their relative importance to Innu subsistence fishing activities and harvest. Selected lakes were located inland, remote from human settlements and developments (such as roads) and thus from point sources of anthropogenic pollution (Fig. 1-3). One site (Ashuapamatikuan Lake) was located in the 12,272km^2 Kanairiktok river system, while the other three (Enakapeshakamau, Papauakamau and Mistashini

Lakes) were part of the Eagle River watershed, draining over 10,500km^2 of the Labrador landscape (Anderson 1985). Labrador is characterized by a cold continental climate with mean annual temperatures of -1.2°C, peaking in July (monthly mean of +13.7°C), and reaching lowest averages in January (-18.4°C). Total annual precipitation averages 975mm, with annual means of 542mm and 471cm falling as rain and snow, respectively (Environment Canada 2004b). The region is typically under snow cover from late October until late May to early June, during which time lakes are ice covered. The ice-free period for Labrador lakes is thus short, lasting between four and five months (Scruton 1984). The four study lakes drained east, were oligotrophic, supported relatively simple biological communities, and differed by their morphometry (Table 3-4). Riparian vegetation at all sites was dominated by black spruce (*Picea mariana*), in some areas associated with balsam fir (*Abies balsamea*). Igneous rock surfaces characterize the easternmost Canadian Shield region, and exposed precambrian granite is the dominant feature of Labrador bedrock geology (Sutton 1972).

Field Sampling

Lakes were accessed by float plane in July of 2002 and 2003 and sampled for fish in both years. In 2003 only, lakes were sampled for water quality, aqueous mercury and methylmercury, periphyton, suspended particulate and plankton. Lakes were physically characterized using GIS for lake perimeter (LPeri), surface area (LArea), and drainage area (DArea). Maximum depth (Zmax) was recorded on-site as the deepest point measured over repeated depth transects using a Garmin GPS-map 188 sounder. Two water column sampling stations were determined for each lake. pH and temperature profiles with depth were determined using a Fondriest YSI-6600 in-situ profiler. Water

samples for chlorophyll *a* (Chla) and suspended particulate matter (SPM) determination were collected using an electric pump within the photic water layer. Three one-liter sub-samples were collected from an integrated 20 liter sample for pelagic Chla determination. Sub-samples were filtered onto GF/F glass fibre filters and frozen pending analysis. SPM were collected on pre-combusted GF/F glass fibre filters from pre-filtered (≤210 and ≤64μm) water samples. Depending on site, one to three liters were filtered to estimate SPM concentrations. Tangential flow filtration of large water volumes (≥100liters) was also used to concentrate SPM for total Hg determination ($[Hg]_{SPM}$) (modified from Montgomery et al. 2000). Concentrated SPM was collected on pre-combusted GF/F glass fiber filters. Pre-filtered water samples (first through a 0.7μm GF/F glass fiber filter, then through a 0.45μm GN-6 mixed cellulose esther Gelman® filter) were collected within the photic water layer and below (i.e. ±1m above lake bottom) for aqueous mercury ($[Hg]_{(aq)}$) and methylmercury ($[MeHg]_{(aq)}$) determination. Water samples for Hg determination were taken using a manually operated peristaltic pump with Masterflex® silicone tubing, and collected in small (250ml) Teflon® containers previously soaked with 7% NaOH and 1N HCl solutions and rinsed with NANOpure® water. Bulk plankton was sampled by repeated vertical tows through the photic layer, using a 53μm-mesh plankton net (except in one lake (Mistashini) where shallow conditions imposed horizontal tows). Samples were rinsed with deionized water, size-fractionated on Nitex screens (≥500, 200, 100, and 53μm), and left on ice for 4 to 6 hours to depurate. The 53-99μm plankton fraction was filtered onto pre-combusted GF/F glass fiber filters and frozen. Rock surfaces were the principal littoral periphyton substrate in all study lakes. Periphyton was brushed from

littoral rock surfaces between 0.5 and 0.8m depth and collected along with pre-filtered (≤75μm) *in situ* water (modified from Desrosiers et al. (2006a)). Two periphyton sampling stations were chosen for each, and a total surface of 299cm^2 was brushed at each station. Station-specific samples were mixed at the field lab and sub-sampled (50 to 100ml) for filtration on pre-combusted GF/F glass fibre filters. Fish were collected using experimental gill nets (gangs of 5 nets of varying mesh size) and hand-held dip-nets (small littoral fish). Specimens were sampled on-site for white (dorsal) muscle and aging structures (opercula (for White and Long Nose Suckers) and cleithra (Northern Pike), which were placed in sterile polyethylene sampling bags. Fork length, weight, sex and maturity stage were recorded on site for all fish. Northern Pike (NP) and Long Nose Sucker (LNS) were sampled in the four study lakes. White Sucker (WS) was only sampled in the three lakes of the Eagle river watershed. All samples were frozen pending analysis.

Laboratory Analysis

SPM concentrations were measured as dry weights. Periphyton biomass (Biomass(peri)) was estimated as ash free dry weight (AFDW). Pelagic and periphyton Chla (Chla(pel) and Chla(peri)) was extracted overnight by soaking filters in 90% acetone at 4°C and in the dark. Chla concentrations were then measured as fluorescence on a Turner Designs TD10 fluorometer. Periphyton percent chlorophyll *a* (%Chla(peri)) is the average of Chla(peri):Biomass(peri) ratios calculated for replicate periphyton filters, expressed as a percentage. Fish were aged by C. Robertson at the Ontario Federation of Anglers & Hunters.

Stable isotope analysis

All samples were lyophilised prior to stable isotope analysis. Fish samples (white muscle tissue) were homogenized using an agate mortar and pestle. Stable isotope ratios of carbon and nitrogen were separately determined for fish (white muscle) samples (n=166) on a Finnigan MAT252 stable isotope ratios mass spectrometer at the stable isotope laboratory in the department of Earth Sciences, Memorial University. Carbon and nitrogen isotopic compositions were separately determined for primary producer (filter) samples (periphyton (n=16), SPM (n=16) and 53μm plankton (n=8)) using a continuous flow stable isotope ratio mass spectrometer and elemental analyzer (Isoprime, GV instruments) at GEOTOP laboratories, Université du Québec à Montréal. Plankton samples analyzed on both mass spectrometry systems and in both laboratories yielded similar isotopic ratios within ±0.18‰ for $\delta^{13}C$, and ±0.27‰ for $\delta^{15}N$. Stable isotopic compositions are measured as the ratio of the heavier to the lighter isotope of an element, and expressed as permil difference (delta notation (δ)) from the same ratio in a standard reference material (i.e. $\delta^{13}C_{fish} = [((^{13}C/^{12}C)_{fish} / (^{13}C/^{12}C)_{VPDB}) - 1] * 10^3$). Values are reported relating to international standards: Vienna Pee Dee belemnite (VPDB) limestone for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. Standard deviation values for day-to-day isotope ratio measurements on a fish (*Salvelinus namaycush*) sample were equivalent to ±0.11‰ for $\delta^{13}C$ and ±0.09‰ for $\delta^{15}N$.

Mercury analysis

Aqueous Hg and MeHg analysis, as well as total Hg determination in SPM ($[Hg]_{SPM}$) and periphyton ($[Hg]_{peri}$) samples, were conducted by atomic fluorescence following the method elaborated and described by Pichet *et al.* (1999). Since lakes were not stratified,

$[Hg]_{aq}$ and $[MeHg]_{aq}$ were averaged over the entire water column. Detection limits for $[Hg]_{aq}$ and $[MeHg]_{aq}$ were 0.2 ng L^{-1} and 0.05 ng L^{-1} respectively. Total Hg concentrations [Hg] were determined for lyophilized fish muscle tissue (n=166) by isotope dilution on a Perkin Elmer ELAN 6100 ICP-MS equipped with a FIAS 400 system. Nearly all (≈99%) Hg in fish muscle tissue is in the form of MeHg (Bloom 1992). Samples were digested by heating spiked (^{201}Hg enriched) samples to 60°C overnight with concentrated HNO_3. HNO_3 was added the following day and samples were digested for 2 more hours. H_2O_2 was added to complete the digestion process. BrCl was added to oxidize all forms of mercury to Hg^{2+}. After 12 hours, the un-reacted BrCl was neutralized by addition of NH_2OH HCl. Samples were then diluted and mercury was reduced from Hg^{2+} to Hg^0 by on-line addition of $NaBH_4$ to generate Hg vapor. The ratio of net counts of ^{202}Hg to ^{201}Hg was used to determine total Hg. QA/QC (μg/g (dry weight)) for DORM-2 = 4.64/4.04, for DOLT-2 = 2.14/2.07. Mean concentration for method blanks was 0.00009 μg/g.

Stable isotope data

Our stable isotope approach is described in details in Chapter 1. Mean isotopic compositions of periphyton and SPM + 53μm-plankton were used as lake-specific littoral and pelagic isotopic baselines, respectively (Table 3-2). These organisms represent bulk Hg pools available to aquatic biota before MeHg/Hg discrimination occurs during trophic transfers (Downs et al 1998). The carbon isotopic composition of littoral and pelagic baselines significantly differed in all lakes (Table 3-2). The nitrogen isotopic composition of baseline organisms were similar among lakes and between habitats within lakes (Table

3-2). Stable isotope ratios of carbon are used as carbon source-flux tracers to estimate fish horizontal resource use as percent reliance on littoral versus pelagic carbon sources in lakes: $\%C_{LITT/PEL} = [(\delta^{13}C_{fish} - \delta^{13}C_{pelagic})/ (\delta^{13}C_{littoral} - \delta^{13}C_{pelagic})] * 100$ (Fry and Sherr 1984). Stable isotope ratios of nitrogen are used as trophic indicators to estimate fish vertical resource use as trophic position: $TrophP = \lambda + (\delta^{15}N_{fish} - \delta^{15}N_{pelagic}) / \Delta^{15}N$ (where λ is the trophic position of baseline organisms (=1) and $\Delta^{15}N$ is equivalent to +3.4‰) (Post 2002a).

Table 3-2. Mean $\delta^{15}N$ and $\delta^{13}C$ isotopic values (±SE) for littoral and pelagic isotopic baselines in the study lakes, with inter-habitat and among lake differences in means.

lakes	littoral	pelagic	inter-habitat			littoral	pelagic	inter-habitat		
	($\delta^{15}N_{littoral}$)	($\delta^{15}N_{pelagic}$)	t	df	p	($\delta^{13}C_{littoral}$)	($\delta^{13}C_{pelagic}$)	t	df	p
Ashua	1.2±0.6	1.7±0.6	0.465	4	0.666	-23.4±0.2	-27.3±0.9	-2.918	4	0.043
Enaka	-0.8±0.1	1.1±0.6	2.303	3	0.105	-22.4±1.1	-27.8±0.6	-4.809	3	0.017
Mista	-0.6±1.0	0.1±1.2	0.334	4	0.755	-18.8±0.9	-27.9±0.5	-10.578	4	<0.001
Papaua	-1.4±0.2	-0.3±0.3	2.363	3	0.099	-19.6±0.4	-28.7±0.3	-17.253	4	<0.001
n	8	14	among lakes $\delta^{15}N$			8	15	among lakes $\delta^{13}C$		
F-ratio	3.78	1.19				9.20	0.96			
p-value	0.116	0.361				0.029	0.446			

Ashua=Ashuapamatikuan Lake, Enaka=Enakapeshakamau Lake, Mista=Mistashini Lake, Papaua=Papauakamau Lake. Sample n=2 for littoral baselines in every lake. Sample n=4 for pelagic baselines (except in Enaka where n=3 for pelagic $\delta^{15}N$ and $\delta^{13}C$ and in Papaua where n=3 for pelagic $\delta^{15}N$).

Data analysis

Fish populations were size-structured for analysis using species-specific biological data (Scott and Crossman 1998) and Hg bioaccumulation trends determined from earlier Labrador Hg studies (Bruce et al. 1979, Scruton 1984). A priori defined size-classes were later adjusted to fit age data according to the following criteria. In every species, size class I (scI) represents age 0 to 2+ individuals, size class II (scII) comprises average-size

fish, and size class III (scIII) are larger-than-average size fish. Species-specific size ranges for the three size classes are shown in Table 3-3.

Table 3-3. Species specific size ranges (as fork length) for each size category.

Specie	Size class	Size range (mm)
Long Nose Sucker (LNS)	I	≤100
(Aequivocus consumer)	II	101-349
	III	≥350
Northern Pike (NP)	I	≤300
(Quis consumer)	II	301-699
	III	≥700
White Sucker (WS)	I	≤100
(Ubi consumer)	II	101-379
	III	≥380

"Population" here refers to all fish from a given species sampled in a lake. "Community" applies to the entire fish assemblage sampled in a lake. "Trophic plateau" describes a lack of significant variation in trophic position with fork length or age. The fish community composition of Ashuapamatikuan Lake differed from lakes of the Eagle River watershed (Enakapeshakamau, Papauakamau and Mistashini lakes). Community type (Comtype) was used as a dummy variable (0=Ashuapamatikuan Lake and 1=all three other lakes) to assess potential community composition effects on Hg accumulation in the two species (NP and LNS) found in the four study lakes.

For each fish species/autecological type, data analysis followed a sequence of four steps. (1) *Biological features and bi-dimensional resource use.* In this section, differences in growth rates among lakes or between community types were examined by comparing slopes of fork length-at-age relationships using GLM procedure. Relationships between

vertical trophic position (TrophP) and horizontal littoral-pelagic resource use ($\%C_{LITT/PEL}$), and between TrophP and $\%C_{LITT/PEL}$ and fish fork length (FL) or age, were tested using linear regression analysis. GLM-procedure was used to determine whether significant relationships differed among lakes. Pearson correlation was used to determine whether fish TrophP and $\%C_{LITT/PEL}$ were significantly correlated to any of the measured lake characteristics. (2) *Among-lake differences in Hg concentrations.* Differences in mercury concentrations ([Hg]) among lakes and between community types were assessed by size class using one-way ANOVAS or t-tests. In ANOVAS, pairwise comparisons were conducted using Scheffe's test. Fish Hg data was log-transformed (base 10) in order to reduce residuals heteroscedasticity. (3) *Patterns of Hg accumulation with biological features and bi-dimensional resource use.* Linear regression was used to assess relationships between fish [Hg] and fork length, age, $\%C_{LITT/PEL}$ and TrophP. Where significant relationships were found, GLM procedure was used to determine whether patterns differed among lakes. Pearson correlation was used to determine whether slopes values of significantly lake-to-lake patterns were related to any species or lake specific characteristics. (4) *Best linear model for predicting Hg levels.* Forward stepwise linear regression procedures were performed to identify the best predictors of [Hg] by species/autecological type. An alpha of 0.25 was used as inclusion criterion in the stepwise procedure.

Minitab® software was used to assess the normality and equality of variance of all residuals, to perform stepwise linear regressions, and to generate Pearson correlation matrices with p-values. All other statistical procedures (GLM, ANOVAS, Scheffe's Test, and T-tests) were carried out on SYSTAT® software (Wilkinson 2001).

Study lakes

Physico-chemical and biological characteristics of the study lakes are shown in Table 3-4 with baseline (aqueous, SPM and periphyton) total Hg concentrations. Aqueous Hg concentrations ($[Hg]_{aq}$) were relatively similar among the study lakes. Littoral periphyton total Hg concentrations ($[Hg]_{peri}$) were lower than water column SPM total Hg ($[Hg]_{SPM}$) (t=-3.516, df=12, p=0.004). This indicated spatial (inter-habitat) differences in total Hg availability within lakes.

Table 3-4. Physico-chemical and biological characteristics of the study lakes, with aqueous, SPM and periphyton total Hg concentrations (mean values).

	Ashuapamatikuan	Enakapeshakamau	Mistashini	Papauakamau
Coordinates	54°39'N 62°24'W	53°15'N 59°04'W	52°46'N 59°35'W	52°41'N 59°24'W
Watershed	Kanairiktok River	Eagle River	Eagle River	Eagle River
DArea (km^2)	3433	1240	276.5	323.4
LArea (km^2)	17.21	20.65	6.21	27.43
LPeri (km)	27.75	54.43	10.15	43.94
PAratio	1.61	2.64	1.64	1.60
Zmax (m)	115	26	2	20
pH	6.3	6	5.9	5.8
Secchi (m)	5	7	1.5	2
SPM ($mg\ L^{-1}$)	0.14	0.21	0.93	1.55
Chla(pel) ($\mu g\ L^{-1}$)	0.67	0.82	1.94	2.68
Biomass(peri) ($\mu g/cm^2$)	1492	610	2464	1567
Chla(peri) ($\mu g/cm^2$)	1.82	0.39	1.81	1.95
%Chla(peri)	0.132	0.086	0.078	0.291
$Hg_{(aq)}$ ($ng\ L^{-1}$)	2.17	2.78	2.98	2.89
$MeHg_{(aq)}$ ($ng\ L^{-1}$)	<0.05	<0.05	0.1	0.08
$[Hg]_{SPM}$ ($ng\ g^{-1}$ DW)	407	581	166	348
$[Hg]_{peri}$ ($ng\ g^{-1}$ DW)	5	113	184	19

Legend: DArea=lake drainage area, LArea=lake surface area, LPeri= lake perimeter, PAratio=ratio of LPeri/LArea, Zmax=maximum depth, SPM=Suspended particulate matter concentration, Chla(pel)=pelagic Chla concentration, Biomass(peri)=periphyton biomass, Chla(peri)=periphyton Chla concentrations, %Chla(peri)=(Chla(peri)/Biomass(peri)*100), $Hg_{(aq)}$=aqueous total Hg concentration, $MeHg_{(aq)}$=aqueous methylmercury concentration, $[Hg]_{SPM}$=Suspended particulate mercury concentration, $[Hg]_{peri}$=periphyton mercury concentration.

Results for Quis-type Northern Pike

(1) *Biological features and bi-dimensional resource use*

Table 3-5 shows mean age and FL, isotope data and average [Hg] for NP populations. In NP, community type distinguished between the presence/absence of alternative prey fish found only in Ashuapamatikuan Lake (Lake Trout (*Salvelinus namaycush*) and White Fish (*Coregonus clupeaformis* (Mitchill)). NP growth rates were similar among lakes and community types (GLM (FL*(Age*lake)): n=50, $F_{3,42}$=2.28 p=0.09; GLM (FL*(Age*Comtype)): n=50, $F=_{1,46}$=2.28, p=0.14). NP TrophP was not related to NP $\%C_{LITT/PEL}$ in the study lakes (n=54, $F_{1,52}$=1.91, p=0.18).

Table 3-5. Northern Pike morphometrics (mean Age and FL), isotope data and Hg concentrations (means ± SE) by populations (pop) and size-classes (sc).

		n	Age	FL (mm)	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$	[Hg]
Species total		54	7+	601		3.3 ± 0.1		38 ± 2.8	0.31 ± 0.03
Ashua	pop	18	7+	619	9.5 ± 0.2	3.3 ± 0.1	-25.8 ± 0.3	39 ± 6.7	0.31 ± 0.04
	scI	1	2+	135	7.0	3.0	-22.9	100	0.04
	scII	10	5+	557	9.4 ± 0.3	3.3 ± 0.1	-26.2 ± 0.4	31 ± 9.8	0.24 ± 0.04
	scIII	7	9+	776	10 ± 0.1	3.4 ± 0.04	-25.7 ± 0.1	43 ± 3.8	0.43 ±0.03
Enaka	pop	5	4+	477	7.6 ± 0.5	2.9 ± 0.1	-24.0 ± 0.1	70 ± 2.1	0.23 ± 0.07
	scI	1	1+	192	6.2	3.0	-24.3	65	0.03
	scII	3	5+	487	7.7 ± 0.4	3.0 ± 0.1	-23.9 ± 0.2	72 ± 2.9	0.22 ± 0.07
	scIII	1	6+	732	8.7	3.0	-24.0	69	0.44
Mista	pop	21	7+	562	7.6 ± 0.4	3.2 ± 0.1	-25.0 ± 0.2	32 ± 2.2	0.29 ± 0.06
	scI	6	1+	165	5.1 ± 0.3	2.5 ± 0.1	-24.4 ± 0.2	38 ± 1.9	0.03 ± 0.004
	scII	8	8+	604	8.5 ± 0.1	3.5 ± 0.03	-25.7 ± 0.4	24 ± 4.0	0.23 ± 0.02
	scIII	7	11+	855	8.8 ± 0.1	3.6 ± 0.03	-24.6 ± 0.2	36 ± 1.8	0.59 ± 0.12
Papaua	pop	10	8+	715	9.3 ± 0.2	3.8 ± 0.1	-25.6 ± 0.3	35 ± 2.8	0.41 ±0.08
	scI	0							
	scII	3	4+	430	8.6 ± 0.6	3.6 ± 0.2	-26.1 ± 0.8	29 ± 9.1	0.14 ± 0.04
	scIII	7	10+	837	9.6 ± 0.1	3.9 ± 0.02	-25.4 ± 0.1	37 ± 1.3	0.52 ± 0.09

Ashua=Ashuapamatikuan Lake, Enaka=Enakapeshakamau Lake, Mista=Mistashini Lake, Papaua=Papauakamau Lake. n=sample number, TrophP=trophic position, $\%C_{LITT/PEL}$=percent reliance on littoral versus pelagic carbon source.

NP $\%C_{LITT/PEL}$ was not related to NP FL or age in the study lakes ($\%C_{LITT/PEL}$*FL: n=54, $F_{1,52}$=0.15, p=0.70; $\%C_{LITT/PEL}$*age: n=50, $F_{1,48}$=0.11, p=0.74). Trophic position varied with FL and age depending on lake (GLM (TrophP*(FL*lake)) n=54, $F_{3,46}$=3.79, p=0.016; GLM (TrophP*(age*lake)) n=50, $F_{3,42}$=4.82, p=0.006). Distinct patterns of increasing TrophP with FL and age characterized NP in Papauakamau Lake (Fig. 3-3).

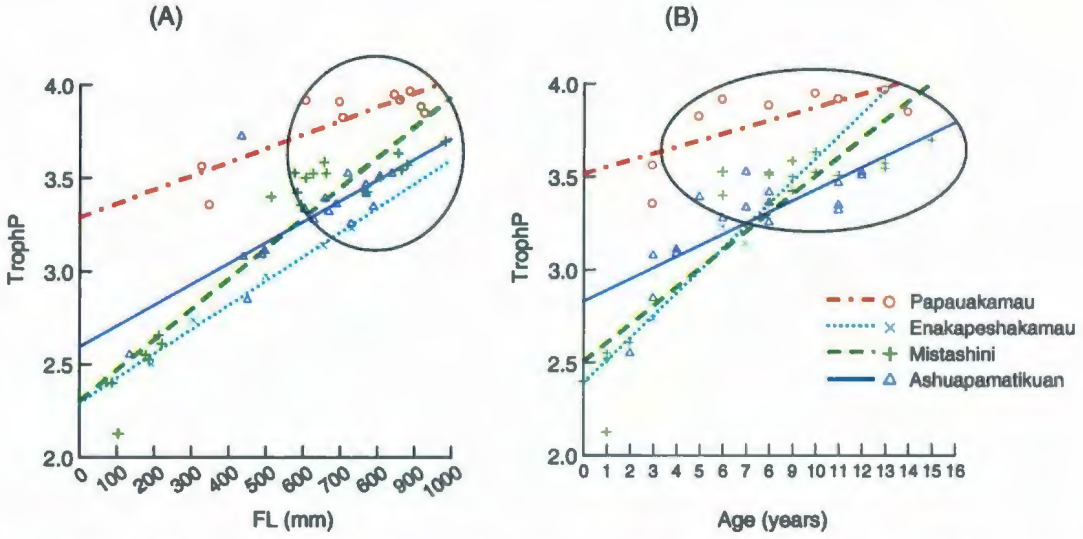


Fig. 3-3. Biological features and bi-dimensional resource use in Quis-type Northern Pike. (A) Site-specific variations in TrophP with FL (Papaua: TrophP=3.28 + 0.000743FL (n=10, F=18.95, p=0.002, r^2=0.67), Enaka: TrophP=2.29 + 0.00131FL (n=5, F=213.72, p=0.001, r^2=0.98), Mista: TrophP=2.30 + 0.00163FL (n=21, F=133.56, p<0.001, r^2=0.87), Ashua: TrophP=2.59 + 0.00112FL (n=18, F=18.76, p=0.001, r^2=0.51)). (B) Site-specific variations in TrophP with age (Papaua: TrophP=3.51 + 0.0357age (n=9, F=7.27, p=0.031, r^2=0.44), Enaka: TrophP=2.39 + 0.121age (n=4, F=28.75, p=0.033, r^2=0.90), Mista: TrophP=2.50 + 0.100age (n=20, F=73.52, p<0.001, r^2=0.79), Ashua: TrophP=2.83 + 0.0603age (n=17, F=23.36, p<0.001, r^2=0.58)). Circled areas indicate lake-specific trophic plateaus.

NP was characterized by a trophic plateau in three lakes (a small sample number (n=5) did not permit to evaluate the presence of such trophic plateau in Enakapeshakamau Lake). TrophP no longer increased with FL in ≥600mm NP in Papauakamau and Mistashini lakes (Papaua: n=8, $F_{1,6}$=0.04, p=0.84; Mista: n=11, $F_{1,9}$=3.60, p=0.09) and in

≥650mm NP in Ashuapamatikuan lake (Ashua: n=10, $F_{1,8}$=3.03, p=0.12) (Fig. 3-3A). Likewise, NP TrophP did not increase with age beyond age 5 in Ashuapamatikuan and Papauakamau lakes (for age≥5 NP in Ashua: n=12, $F_{1,10}$=1.87, p=0.20; in Papaua: n=7, $F_{1,5}$=0.65, p=0.46), and beyond age 10 in Mistashini Lake (for age≥10 NP in Mista: n=6, $F_{1,4}$=1.59, p=0.28) (Fig. 3-3B). NP TrophP did not correlate to any of the lake characteristics. $\%C_{LITT/PEL}$ by NP was positively correlated to lake perimeter to area ratio (n=4, r=0.980, p=0.02).

(2) ***Among-lake differences in Hg concentrations.***

NP [Hg] did not differ among lakes or between community types (Fig.3-4a).

(3) ***Patterns of Hg accumulation with biological features and bi-dimensional resource use***

All fish considered, NP [Hg] increased with FL, TrophP and age (Fig. 3-5, Table 3-6). Hg-age relationships differed among lakes (GLM (Log_{10}Hg*(Age*lake)): n=50, $F_{3,42}$=5.18, p=0.004) (Fig. 3-5C). Lake-specific slopes of Hg-age relationships were positively related to lake PAratio (n=4, r=0.950, p=0.050). In ≥600mm NP (trophic plateau), TrophP no longer explained NP [Hg] (Log_{10}Hg*TrophP in ≥600mm NP: n=33, $F_{1,31}$=2.43, p=0.13). Still NP [Hg] increased with FL within this size range (Log_{10}Hg*FL in ≥600mm NP: n=33, $F_{1,31}$=68.78, p<0.001) and varied linearly with $\%C_{LITT/PEL}$ depending on lake (GLM (Log_{10}Hg*($\%C_{LITT/PEL}$*lake)) in ≥600mm NP: n=33, $F_{3,25}$=3.39, p=0.030). Linear patterns of Hg accumulation with $\%C_{LITT/PEL}$ were significant in three lakes, depending on size. [Hg] increased with littoral resource use in ≥600mm NP in Papauakamau lake and in ≥490mm NP in Mistashini and Ashuapamatikuan lakes (Fig. 3-5D and Table 3-6).

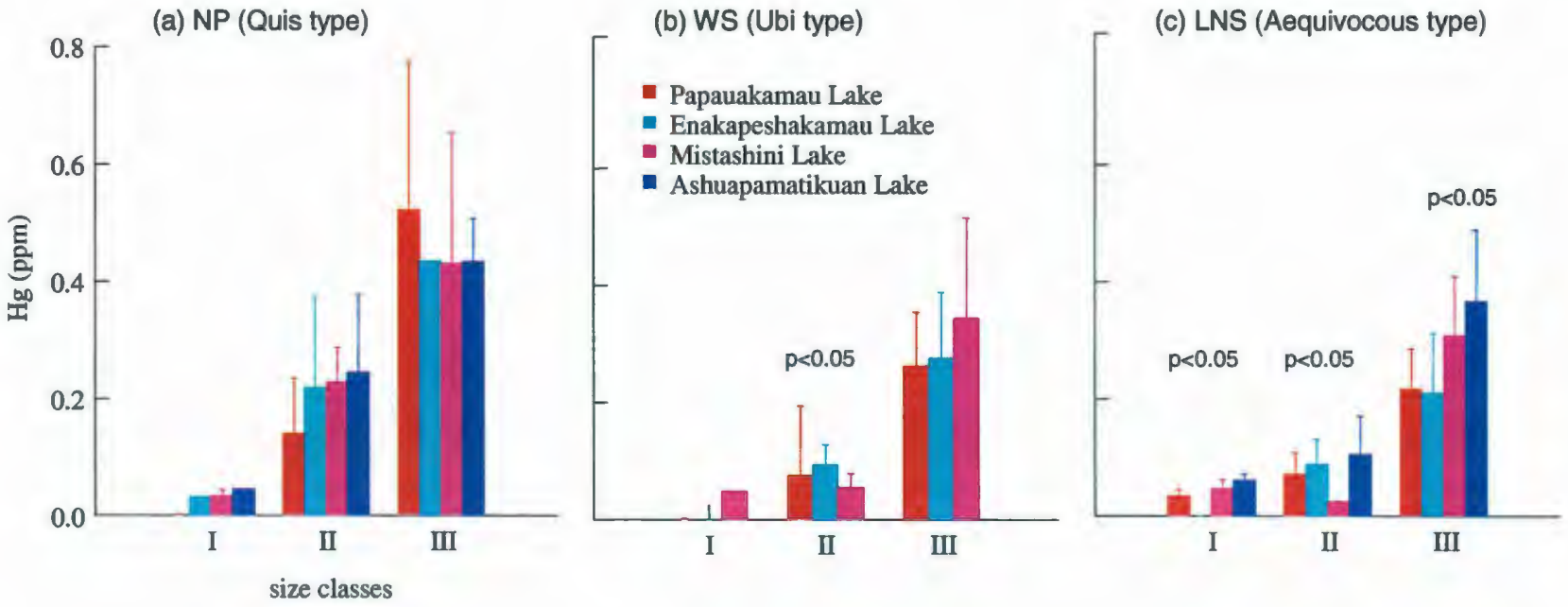


Fig. 3-4. Average Hg concentrations by species, lake and size-class in (a) Quis-type Northern Pike, (b) Ubi-type White Sucker and (c) Aequivocous-type Long Nose Sucker. Significant differences among lakes are identified by p-values<0.05. Error bars = Stdev.

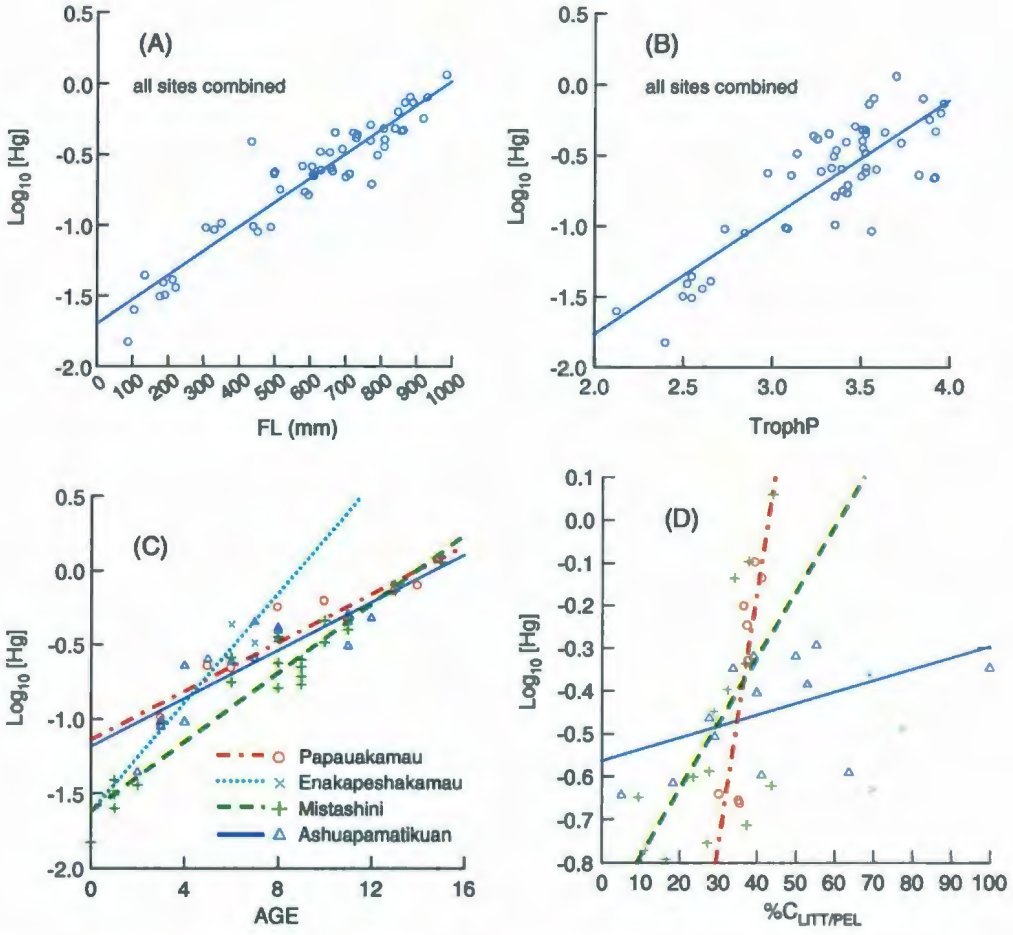


Fig. 3-5. Patterns of Hg accumulation with biological features and bi-dimensional resource use in Quis-type NP. (A) Hg accumulation with FL. (B) Hg accumulation with vertical trophic position (TrophP). (C) Lake-specific patterns of Hg accumulation with age. (D) Lake-specific patterns of Hg accumulation with horizontal reliance on littoral versus pelagic carbon sources ($\%C_{LITT/PEL}$).

Table 3-6. Patterns of Hg accumulation in Quis-type Northern Pike (see Fig. 3-5).

Response variable = $Log_{10}Hg$ in Northern Pike

predictor	site(s)	linear equation	n	F-ratio	p-value	r^2_{adj}	note(s)
FL	all	$Log_{10}Hg = -1,70 + 0,00172$ FL	54	449.26	<0.001	0.894	
TrophP	all	$Log_{10}Hg = -3,42 + 0,828$ TrophP	54	126.00	<0.001	0.702	
Age	Ashua	$Log_{10}Hg = -1,18 + 0,0809$ age	17	41.03	<0.001	0.714	
Age	Enaka	$Log_{10}Hg = -1,62 + 0,183$ age	4	28.56	0.033	0.902	
Age	Mista	$Log_{10}Hg = -1,62 + 0,116$ age	20	245.99	<0.001	0.928	
Age	Papaua	$Log_{10}Hg = -1,14 + 0,0818$ age	9	48.94	<0.001	0.857	
$\%C_{LITT/PEL}$	Ashua	$Log_{10}Hg = -0,677 + 0,00466\ \%C_{LITT/PEL}$	14	6.05	0.03	0.280	≥490mm NP only
$\%C_{LITT/PEL}$	Mista	$Log_{10}Hg = -0,939 + 0,0153\ \%C_{LITT/PEL}$	15	8.10	0.014	0.337	≥490mm NP only
$\%C_{LITT/PEL}$	Papaua	$Log_{10}Hg = -2.55 + 0.0591\%C_{LITT/PEL}$	8	10.08	0.019	0.565	≥600mm NP only

(4) *Best linear model for predicting Hg levels in Quis-type NP*

Stepwise linear regressions identified NP biological features (FL and Age), estimates of vertical and horizontal resource use (TrophP and $\%C_{LITT/PEL}$) and lake SPM concentrations as significant predictors of NP [Hg] (Table 3-7). Together, these variables explained 95% of the variability in NP Hg levels across the study lakes. (Fig. 3-11).

Table 3-7. Results of stepwise linear regressions for Quis-type Northern Pike.

Response variable = Log_{10}Hg in Northern Pike

step 1 r^2_{adj}=0.928			step 2 r^2_{adj}=0.934			step 3 r^2_{adj}=0.938			step 4 r^2_{adj}=0.946			step 5 r^2_{adj}=0.949		
predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value
FL	25.21	<0.001	FL	26.43	<0.001	FL	11.77	<0.001	FL	9.49	<0.001	FL	5.19	<0.001
			$\%C_{LITT/PEL}$	2.33	0.024	$\%C_{LITT/PEL}$	2.82	0.007	$\%C_{LITT/PEL}$	2.69	0.010	$\%C_{LITT/PEL}$	2.30	0.026
						TrophP	1.95	0.057	TrophP	3.32	0.002	TrophP	3.68	0.001
									SPM	-2.75	0.009	SPM	-3.16	0.003
												Age	1.99	0.052

Results for Ubi-type White Sucker

(1) *Biological features and bi-dimensional resource use*

Table 3-8 shows mean age and FL, isotope data and average [Hg] for WS populations. Growth rates differed among lakes in WS (GLM (FL*(age*lake)): n=52, $F_{2,46}$=12.52, p<0.001) (Fig. 3-6A). Fork length-at-age relationships were only significant in two lakes (in Mistashini and Enakapeshakamau). WS TrophP varied negatively with WS $\%C_{LITT/PEL}$ in the study lakes (Fig. 3-6B). $\%C_{LITT/PEL}$ by WS was not related to FL or age ($\%C_{LITT/PEL}$*FL: n=54, $F_{1,52}$=0.00, p=1.00; $\%C_{LITT/PEL}$*age: n=52, $F_{1,50}$=0.10, p=0.76). TrophP increased with FL (Fig.3-6C), but did not vary with WS age (n=52, $F_{1,50}$=1.18, p=0.28). WS TrophP did not correlate to any of the lakes characteristics. $\%C_{LITT/PEL}$ was positively correlated to lake secchi depth (n=3, r=1.000, p=0.005) and drainage area (n=3, r=0.999, p=0.020).

Table 3-8. White Sucker morphometrics (mean Age and FL), isotope data and Hg concentrations (means ± SE) by populations (pop) and size-classes (sc).

		n	Age	FL (mm)	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$	[Hg]
species total		54	13+	378		2.7 ± 0.04		47 ± 2.4	0.20 ± 0.02
Enaka	pop	19	11+	359	5.9 ± 0.1	2.4 ± 0.02	-24.3 ± 0.2	64 ± 3.1	0.18 ± 0.03
	scI	0							
	scII	10	8+	290	5.9 ± 0.1	2.4 ± 0.03	-24.5 ± 0.2	60 ± 4.4	0.09 ± 0.01
	scIII	9	16+	436	5.8 ± 0.1	2.4 ± 0.04	-24.1 ± 0.2	68 ± 4.0	0.28 ± 0.04
Mista	pop	21	13+	370	5.8 ± 0.1	2.7 ± 0.04	-24.5 ± 0.2	37 ± 2.7	0.20 ± 0.04
	scI	1	≤2+	65	4.5	2.0	-25.8	23	0.05
	scII	9	7+	326	6.0 ± 0.2	2.7 ± 0.1	-24.3 ± 0.5	40 ± 5.4	0.05 ± 0.008
	scIII	11	18+	434	5.8 ± 0.1	2.7 ± 0.03	-24.6 ± 0.2	37 ± 2.5	0.34 ± 0.05
Papaua	pop	14	14+	414	6.8 ± 0.1	3.1 ± 0.03	-25.1 ± 0.3	40 ± 3.8	0.23 ± 0.03
	scI	0							
	scII	2	10+	353	6.7 ± 0.4	3.0 ± 0.1	-26.1 ± 0.1	29 ± 0.7	0.07 ± 0.05
	scIII	12	15+	424	6.8 ± 0.1	3.1 ± 0.04	-25.0 ± 0.4	41 ± 4.2	0.26 ± 0.03

See Legend in Table 3-5.

(2) *Among-lake differences in Hg concentrations*

[Hg] differed among lakes in average-size (scII) WS (n=21, $F_{2,18}$=4.49, p=0.026) (Fig. 3-4b). [Hg] were higher in Enakapeshakamau relative to Mistashini lake within this size range.

(3) *Patterns of Hg accumulation with biological features and bi-dimensional resource use*

WS [Hg] increased with FL and age but did not vary with TrophP or $\%C_{LITT/PEL}$ (Fig. 3-7, Table 3-9). When the only juvenile (scI) WS sampled in the study lakes was removed from analysis, patterns of increasing [Hg] with FL were lake-specific (GLM (LogHg*(FL*lake)): n=53, $F_{2,47}$=6.11, p=0.004) (Fig. 3-7C, Table 3-9). Slopes values of Hg-FL relationships were negatively correlated to WS $\%C_{LITT/PEL}$ (n=3, r=-0.997, p=0.046).

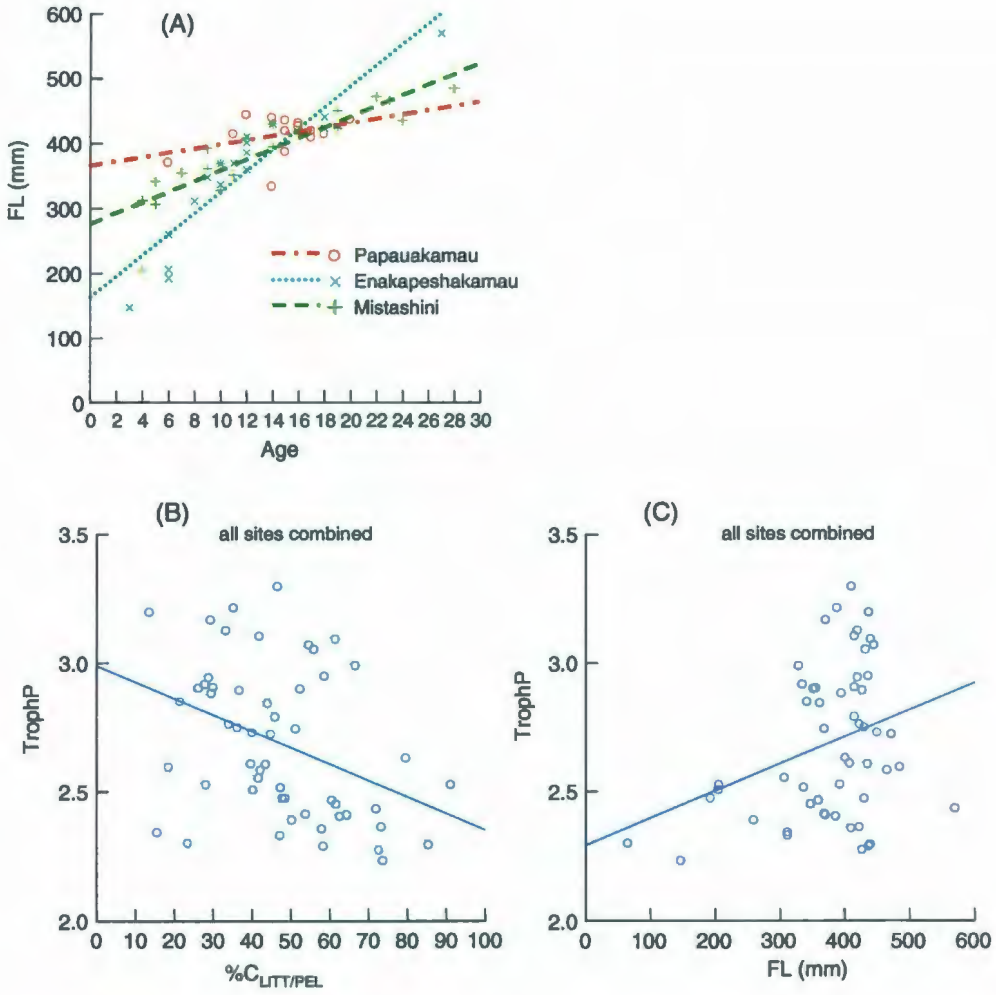


Fig. 3-6. Biological features and bi-dimensional resource use in Ubi-type White Sucker. (A) Among-lake differences in FL-at-age relationships (Papaua: FL=65 + 3.28(age) (n=14, F=1.88, p=0.20); Enaka: FL=163 + 16.2(age) (n=18, F=87.37, p<0.001, r^2=0.84); Mista: FL=276 + 8,22(age) (n=20, F=59.06, p<0.001, r^2=0.75)). (B) Negative relationship between TrophP and littoral resource use: TrophP=2.99 - 0.00638(%$C_{LITT/PEL}$) (n=54, F=9.11, p=0.004, r^2=0.13) (C) Pattern of increasing TrophP with FL: TrophP=2.29 + 0.00105(FL) (n=54, F=5.68, p=0.021, r^2=0.08)).

(4) *Best linear model for predicting Hg levels in Ubi-type WS*

Stepwise linear regressions only identified WS age as a significant predictor of WS [Hg] in the study lakes. Lake area also positively affected WS Hg, but its effect was not statistically significant (Table 3-10). Together, WS age and lake area explained 63% of the variability in WS Hg across the study lakes (Fig. 3-11).

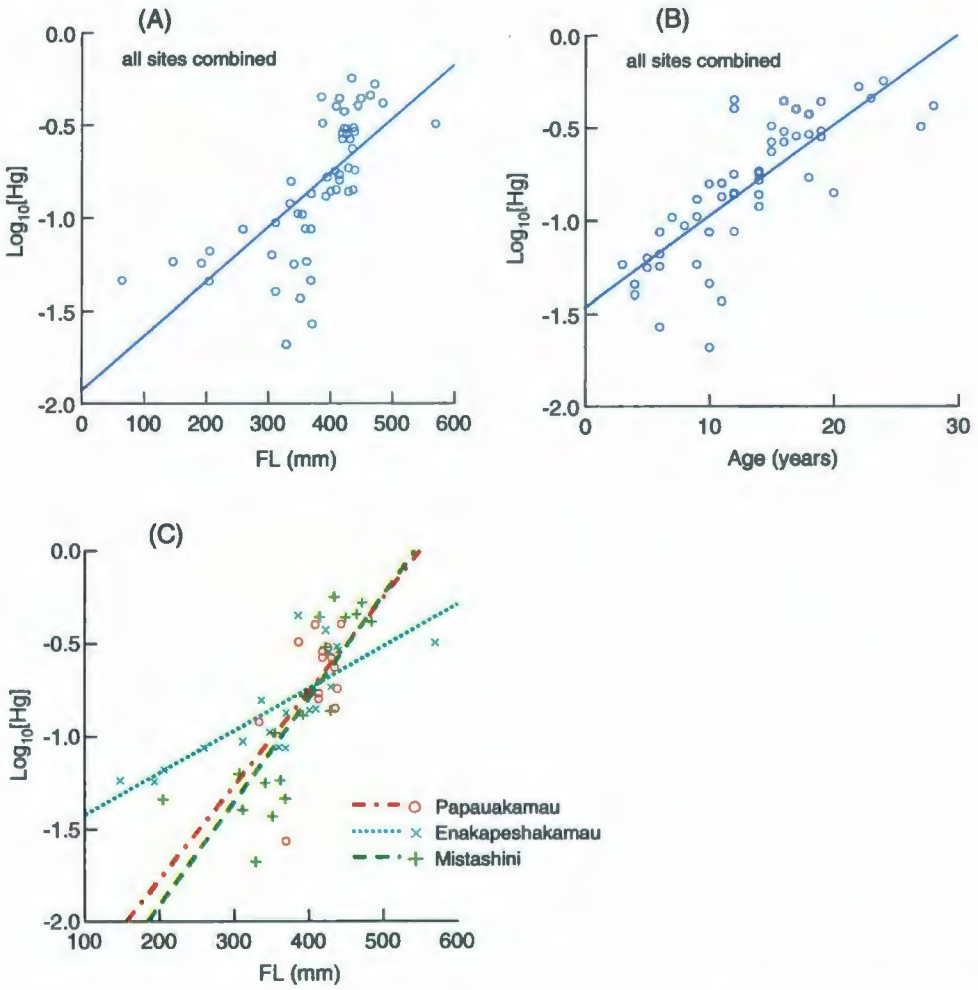


Fig. 3-7. Patterns of Hg accumulation with biological features in Ubi-type WS. (A) Hg accumulation with FL. (B) Hg accumulation with age. (C) Lake-specific patterns of Hg accumulation with FL in >100mm WS.

Table 3-9. Patterns of Hg accumulation in Ubi-type White Sucker (see Fig.3-7).

Response variable = $Log_{10}Hg$ in White Sucker

predictor	site(s)	linear equation	n	F-ratio	p-value	r^2_{adj}	note(s)
FL	all	$Log_{10}Hg$ = - 1,93 + 0,00291 FL	54	48.34	<0.001	0.472	
Age	all	$Log_{10}Hg$ =- 1,47 + 0,0490 AGE	52	83.11	<0.001	0.617	
FL	Enaka	$Log_{10}Hg$ = - 1,65 + 0,00228 FL	19	32.12	<0.001	0.634	scII and scIII WS only
FL	Mista	$Log_{10}Hg$ =- 3,04 + 0,00559 FL	20	38.33	<0.001	0.663	scII and scIII WS only
FL	Papaua	$Log_{10}Hg$ = - 2,80 + 0,00507 FL	14	4.34	0.059	0.204	scII and scIII WS only

Table 3-10. Results of stepwise linear regressions for Ubi-type White Sucker.

Response variable = Log_{10}Hg in White Sucker

step 1 r^2_{adj}=0.617			step 2 r^2_{adj}=0.628		
predictor(s)	t-value	p-value	predictor(s)	t-value	p-value
age	9.12	<0.001	age	9.18	<0.001
			lake area	1.60	0.116

Results for Aequivocous-type Long Nose Sucker

(1) *Biological features and bi-dimensional resource use.*

Table 3-11 shows mean age and FL, isotope data and average [Hg] for LNS populations.

Table 3-11. Long Nose Sucker morphometrics (mean Age and FL), isotope data and Hg concentrations (means ± SE) by populations (pop) and size-classes (sc).

		n	Age	FL (mm)	$\delta^{15}N$	TrophP	$\delta^{13}C$	$\%C_{LITT/PEL}$	[Hg]
Species total		58	12+	331		2.6 ± 0.03		44 ± 3.3	0.18 ± 0.02
Ashua	pop	18	15+	343	7.0 ± 0.1	2.6 ± 0.04	-26.2 ± 0.5	36 ± 9.1	0.24 ± 0.04
	scI	4	1+	70	6.8 ± 0.1	2.5 ± 0.03	-24.5 ± 0.7	72 ± 19	0.06 ± 0.01
	scII	4	5+	247	7.3 ± 0.5	2.7 ± 0.1	-25.8 ± 1.2	31 ± 23	0.10 ± 0.03
	scIII	10	23+	491	6.9 ± 0.2	2.5 ± 0.1	-27.0 ± 0.5	23 ± 10	0.37 ± 0.04
Enaka	pop	17	11+	337	5.7 ± 0.1	2.4 ± 0.02	-25.0 ± 0.2	52 ± 3.3	0.15 ± 0.02
	scI	0							
	scII	8	7+	227	5.7 ± 0.1	2.4 ± 0.03	-24.9 ± 0.3	53 ± 5.3	0.09 ± 0.01
	scIII	9	14+	435	5.7 ± 0.1	2.4 ± 0.03	-25.0 ± 0.2	51 ± 4.5	0.21 ± 0.03
Mista	pop	14	13+	347	5.6 ± 0.2	2.6 ± 0.1	-24.2 ± 0.4	40 ± 4.4	0.19 ± 0.04
	scI	3	1+	70	5.1 ± 0.4	2.5 ± 0.1	-25.9 ± 0.5	22 ± 5.6	0.04 ± 0.01
	scII	3	6+	251	6.2 ± 0.6	2.8 ± 0.2	-22.2 ± 0.8	63 ± 8.3	0.02 ± 0.001
	scIII	8	19+	487	5.5 ± 0.2	2.6 ± 0.1	-24.4 ± 0.2	38 ± 2.5	0.31 ± 0.03
Papaua	pop	9	9+	269	6.3 ± 0.3	2.9 ± 0.1	-24.2 ± 0.4	50 ± 4.5	0.12 ± 0.03
	scI	3	1+	72	5.6 ± 0.3	2.7 ± 0.1	-25.0 ± 0.6	41 ± 6.2	0.03 ± 0.01
	scII	2	4+	221	7.1 ± 0.5	3.2 ± 0.1	-22.7 ± 0.4	66 ± 4.4	0.07 ± 0.02
	scIII	4	15+	441	6.5 ± 0.3	3.0 ± 0.1	-24.3 ± 0.5	48 ± 5.9	0.22 ± 0.03

See Legend in Table 3-5.

In LNS, community type distinguished between the absence/presence of a benthic competitor (in White Sucker) and predation risk (from Northern Pike) (Chapter 1). Populations where LNS co-occurred with WS and was subject to substantial predation risk from NP (in Enakapeshakamau, Mistashini and Papauakamau lakes) are here referred to as "sympatric" LNS populations. These are distinguished from the "allopatric" LNS population of Ashuapamatikuan Lake, where WS was absent and predation risk from NP was lower or nil (as evidenced from stomach contents analysis) (Chapter 1). Growth rates were similar among lakes and community types in LNS (GLM (FL*(Age*lake)): n=55, $F_{3,47}$=2.48 p=0.07; GLM (FL*(Age*Comtype)): n=55, $F=_{1,51}$=3.57, p=0.07). LNS TrophP was not related to LNS $\%C_{LITT/PEL}$ in the study lakes (n=58, $F_{1,56}$=0.001, p=0.97) or to LNS FL or age (for FL: n=58, $F_{1,56}$=0.05, p=0.82; for age: n=55, $F_{1,53}$=0.56, p=0.46). $\%C_{LITT/PEL}$ was faintly negatively related to LNS age (n=55, $F_{1,53}$=5.04, p=0.029) and varied with FL depending on lake and community type (GLM ($\%C_{LITT/PEL}$*(FL*lake)): n=58, $F_{3,50}$=3.22, p=0.030; GLM ($\%C_{LITT/PEL}$*(FL*Comtype)): n=58, $F_{1,54}$=8.94, p=0.004) (Fig. 3-8). Linear $\%C_{LITT/PEL}$-FL relationships were only significant in allopatric LNS from Ashuapamatikuan Lake (Fig. 3-8B and 3-8C). LNS TrophP and $\%C_{LITT/PEL}$ did not correlate to any of the lakes characteristics.

(2) *Among-lake differences in Hg concentrations*

LNS [Hg] differed among lakes in all size classes (scI: n=10, $F_{2,7}$=5.92, p=0.031, scII: n=17, $F_{3,13}$=4.89, p=0.017, scIII: n=31, $F_{3,27}$=4.55, p=0.010) (Fig. 3-4c). In juvenile (scI) LNS, [Hg] were higher in Ashuapamatikuan relative to Papauakamau Lake. In average-size (scII) LNS, [Hg] were higher in Ashuapamatikuan and Enakapeshakamau relative to Mistashini lake. In larger (scIII) adults, [Hg] were greater in Ashuapamatikuan relative to

Enakapeshakamau Lake. Average Hg concentrations were negatively related to LNS $\%C_{LITT/PEL}$ in larger adults (n=4, r=-0.991, p=0.009).

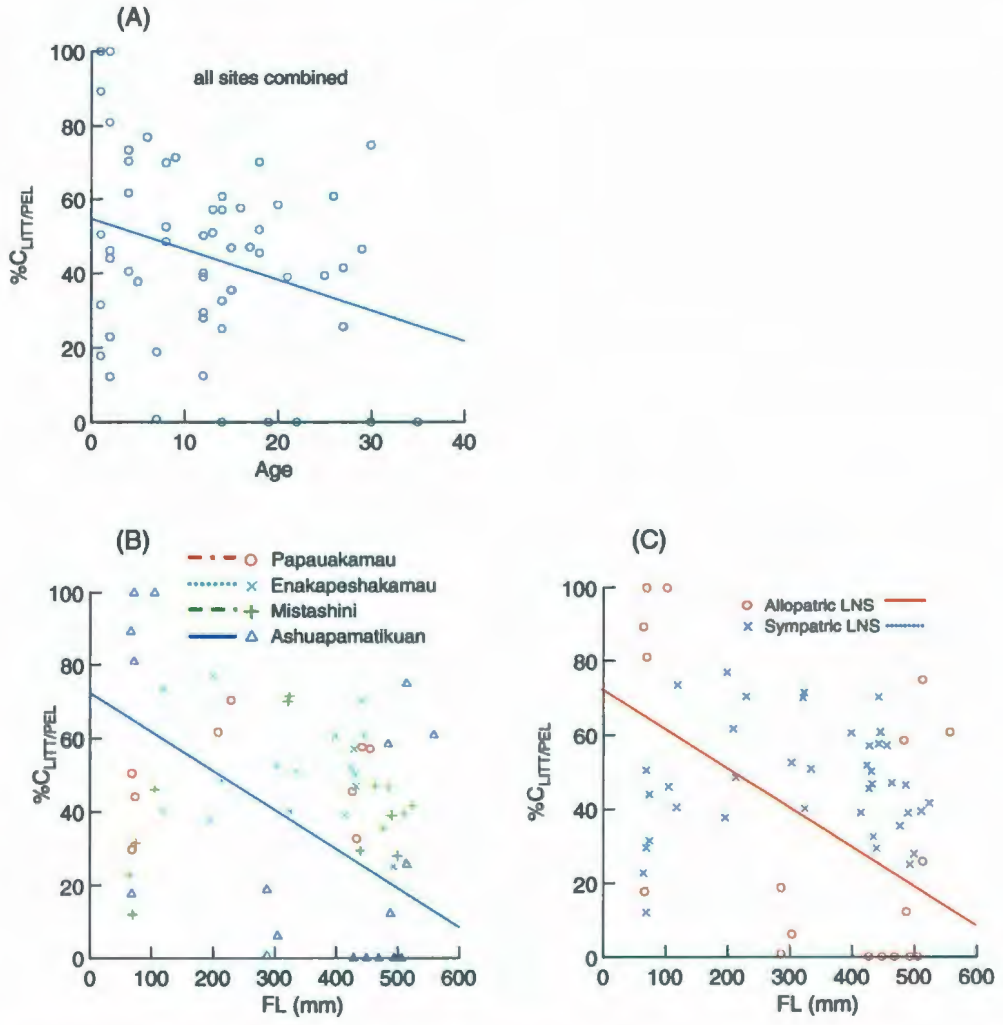


Fig. 3-8. Biological features and bi-dimensional resource use in Aequivocus-type Long Nose Sucker. (A) Linear pattern of decreasing $\%C_{LITT/PEL}$ with LNS age ($\%C_{LITT/PEL}$=54.6 – 0.823(age) (n=55, F=5.04, p=0.029, r^2=0.07)). (B) Lake-specific $\%C_{LITT/PEL}$–FL relationships (Ashua: $\%C_{LITT/PEL}$=72.4 – 0.106(FL) (n=18, F=5.72, p=0.029, r^2=0.22); Enaka: $\%C_{LITT/PEL}$=58.9 – 0.0208(FL) (n=17, F=0.54, p=0.47); Mista: $\%C_{LITT/PEL}$ =32.1 – 0.0226(FL) (n=14, $F_{1,12}$=0.86, p=0.37); Papaua: $\%C_{LITT/PEL}$=46.8 – 0.0113(FL) (n=9, $F_{1,7}$=0.15, p=0.71)). (C) $\%C_{LITT/PEL}$–FL relationships between community types (allopatric LNS: $\%C_{LITT/PEL}$=72.4 – 0.106(FL) (n=18, F=5.72, p=0.029, r^2=0.22); sympatric LNS: $\%C_{LITT/PEL}$=45.5 + 0.0054(FL) (n=40, F=0.12, p=0.73)).

LNS [Hg] also differed between community types. Average [Hg] were higher in allopatric relative to sympatric LNS populations at the juvenile life-stage (n=10, t=2.779, df=8, p=0.024) and in larger adults (n=31, t=2.671, df=29, p=0.012) (Fig. 3-9).

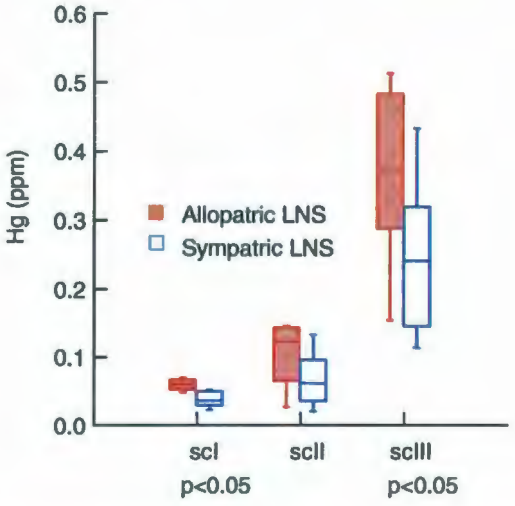


Fig. 3-9. Average [Hg] by size class between community types in Aequivocus LNS.

(3) *Patterns of Hg accumulation with biological features and bi-dimensional resource use*

LNS [Hg] increased with FL and varied with age depending on community type (GLM (Log_{10}Hg*(age*Comtype)): n=55, $F_{1,51}$=5.55, p=0.022) (Fig. 3-10, Table 3-12). [Hg] also varied negatively with LNS $\%C_{LITT/PEL}$ (Fig. 3-10, Table 3-12) but were not related to TrophP.

(4) *Best linear model for predicting Hg levels in Aequivocus-type LNS*

Forward stepwise linear regressions identified FL, age and lake drainage area as significant positive predictors of LNS [Hg], explaining 79% of the variability in LNS Hg levels across the study lakes (Table 3-13, Fig. 3-11).

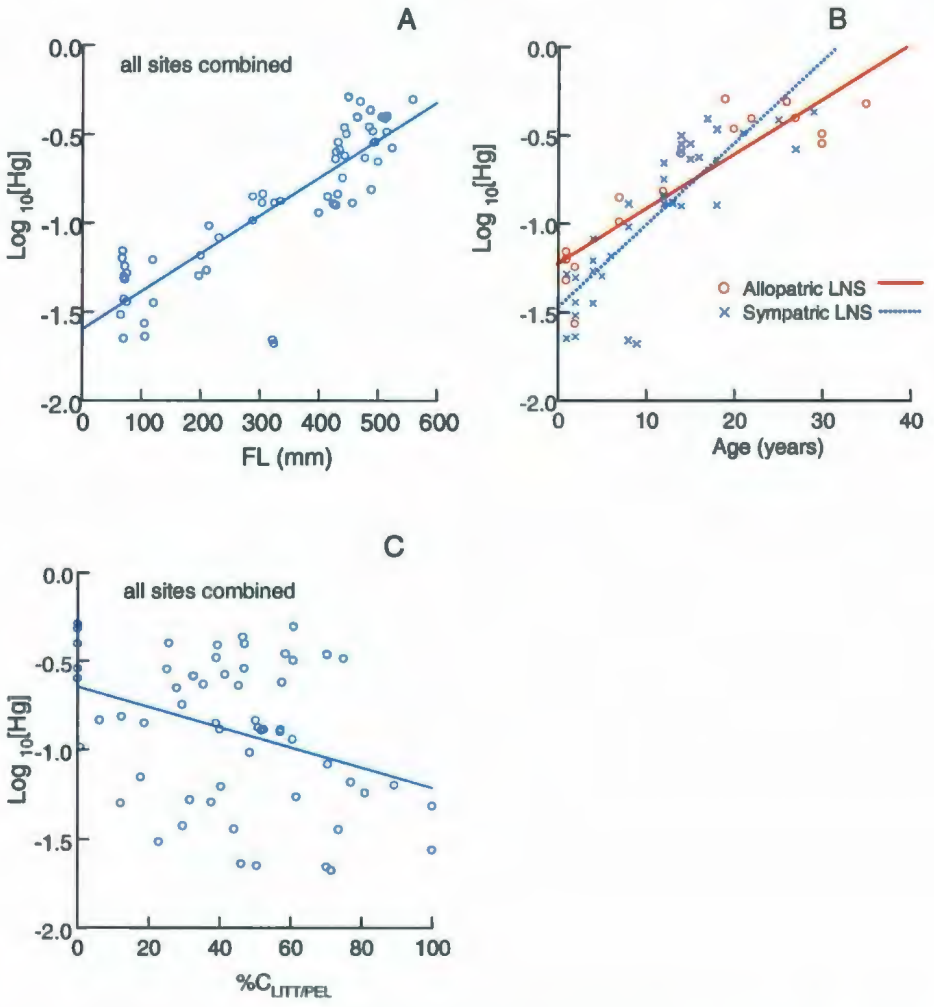


Fig. 3-10. Patterns of Hg accumulation with biological features and bi-dimensional resource use in Aequivocus LNS. (A) Hg accumulation with FL. (B) Community-specific patterns of Hg accumulation with age. (C) Negative relationship between littoral resource use and LNS [Hg].

Table 3-12. Patterns of Hg accumulation in Aequivocus-type Long Nose Sucker (see Fig. 3-10).

Response variable = $Log_{10}Hg$ in Long Nose Sucker

predictor	site(s)	linear equation	n	F-ratio	p-value	r^2_{adj}
FL	all	$Log_{10}Hg = - 1.60 + 0.00212$ FL	58	162.58	<0.001	0.739
Age	sympatric lakes	$Log_{10}Hg = - 1.47 + 0.0466$ age	38	85.60	<0.001	0.696
Age	allopatric lakes	$Log_{10}Hg = -1.23 + 0.0310$ age	17	59.39	<0.001	0.785
$\%C_{LITT/PEL}$	all	$Log_{10}Hg = - 0.646 - 0.00572\ \%C_{LITT/PEL}$	58	7.97	0.007	0.109

Drainage area was a distinct characteristic of Ashuapamatikuan Lake where the LNS population was allopatric. Patterns of Hg accumulation with age also differed between community types (Fig. 3-10B). Community composition, together with FL, explained a similar amount of variability in LNS [Hg] (77%) (model: $Log_{10}Hg(LNS) = -1.49 + 0.00210\ FL - 0.153\ (Comtype)$ ($n=58$, $F_{2,55}=94.30$, $p<0.001$, $r^2_{adj}=0.766$). Separate stepwise linear regressions conducted for sympatric and allopatric LNS populations increased the explained variability in LNS [Hg] to 81% among sympatric lakes and to 85% for allopatric LNS in Ashuapamatikuan Lake (Fig. 3-11). In sympatric populations, [Hg] were explained by LNS FL, age, $\%C_{LITT/PEL}$ and lake maximum depth (Table 3-13). In allopatric LNS, [Hg] were explained by FL. LNS age and $\%C_{LITT/PEL}$ also affected allopatric LNS [Hg], but there effects were not statistically significant (Table 3-13).

Table 3-13. Results of stepwise linear regressions for Aequivocus-type Long Nose Sucker.

Response variable = $Log_{10}Hg$ in Long Nose Sucker

step 1 r^2_{adj}=0.736			step 2 r^2_{adj}=0.771			step 3 r^2_{adj}=0.785		
predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value
FL	12.32	<0.001	FL	3.90	<0.001	FL	3.90	<0.001
			Age	2.99	0.004	Age	2.99	0.004
						Darea	2.12	0.039

Response variable = $Log_{10}Hg$ in sympatric Long Nose Sucker

step 1 r^2_{adj}=0.712			step 2 r^2_{adj}=0.741			step 3 r^2_{adj}=0.765			step 4 r^2_{adj}=0.809		
predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value
FL	9.61	<0.001	FL	2.68	0.011	FL	2.92	0.006	FL	2.77	0.009
			Age	2.24	0.032	Age	2.23	0.032	Age	3.02	0.005
						$\%C_{LITT/PEL}$	-2.17	0.037	$\%C_{LITT/PEL}$	-3.31	0.002
									Zmax	2.98	0.005

Response variable = $Log_{10}Hg$ in allopatric Long Nose Sucker

step 1 r^2_{adj}=0.846			step 2 r^2_{adj}=0.863			step 3 r^2_{adj}=0.870		
predictor(s)	t-value	p-value	predictor(s)	t-value	p-value	predictor(s)	t-value	p-value
FL	9.42	<0.001	FL	3.08	0.008	FL	2.37	0.034
			Age	1.69	0.113	Age	1.93	0.076
						$\%C_{LITT/PEL}$	-1.34	0.202

Quis type Northern Pike:

$\mathbf{Log_{10}Hg(NP) = - 2.443 + 0.00105(FL) + 0.00166(\%C_{LITT/PEL}) + 0.309(TrophP) - 0.112(SPM) + 0.0178(Age)}$

($n=50$, $F_{5,44}=183.98$, $p<0.001$, $r^2_{(adj)}=0.949$)

Ubi type White Sucker:

$\mathbf{Log_{10}Hg(WS) = - 1.555 + 0.0486(age) + 0.0056(LArea)}$

($n=52$, $F_{2,49}=44.13$, $p<0.001$, $r^2_{(adj)}=0.628$)

Aequivocus type Long Nose Sucker (all fish considered):

$\mathbf{Log_{10}Hg(LNS) = - 1.615 + 0.00144(FL) + 0.0145(age) + 0.00004(DArea)}$

($n=55$, $F_{3,51}=66.80$, $p<0.001$, $r^2_{(adj)}=0.785$)

Aequivocus type Long Nose Sucker (allopatric population):

$\mathbf{Log_{10}Hg(LNS) = - 1.28 + 0.00109(FL) + 0.0133(age) - 0.00153(\%C_{LITT/PEL})}$

($n=17$, $F_{3,13}=36.74$, $p<0.001$, $r^2_{(adj)}=0.870$)

Aequivocus type Long Nose Sucker (sympatric populations):

$\mathbf{Log_{10}Hg(LNS) = - 1.436 + 0.00114(FL) + 0.0267(age) - 0.0068\ (\%C_{LITT/PEL}) + 0.00864(Zmax)}$

($n=38$, $F_{4,33}=40.27$, $p<0.001$, $r^2_{(adj)}=0.809$)

Fig. 3-11. Best linear models for predicting Hg levels in fish species classified by autecological types.

DISCUSSION

Horizontal cross-habitat foraging affects Hg bioaccumulation in fish

Our study confirms the influence of horizontal littoral-pelagic foraging for determining Hg bioaccumulation in lake fish. As expected from the non-linear nature of cross-habitat feeding patterns in mobile consumers (chapter 1), this influence was both species and life-stage specific. Littoral resource use was a positive predictor of Hg concentrations in Northern Pike. Greater reliance on littoral prey caused elevated Hg levels in this littoral predator (Scott and Crossman 1998). Patterns of Hg accumulation with littoral resource use explained between 28% and 57% of the variability in Hg levels in adult Northern

Pike, depending on lake. These patterns were linked to the reaching of a trophic plateau in adult life-stages (i.e. in ≥600-650mm Northern Pike). Average plateau trophic positions differed among lakes. This indicated that littoral-pelagic differences in Hg exposure were not independent from among-lake differences in vertical resource use related to body size. The consumption of larger and more contaminated littoral prey with increasing size, probably explained greater Hg uptake via littoral dietary pathways in larger Pike. In White Sucker, littoral-pelagic foraging only indirectly explained among-lake patterns of Hg accumulation with body size. Hg-FL relationships demonstrated that Hg concentrations in smaller (101-400mm) White Sucker were comparatively greater in Enakapeshakamau Lake, where the species relied more upon littoral prey (Fig. 3-7C). This suggested greater Hg exposure via littoral dietary pathways in White Sucker. The lack of a direct relationship between Hg concentrations and littoral-pelagic resource use however, indicates that the effect of horizontal foraging was strongly influenced by lake-specific factors and was highly variable within lakes in this species. In Long Nose Sucker, littoral resource use was a negative predictor of Hg body burdens. Lower Hg exposure and uptake via littoral dietary pathways in this species, was likely related to the consumption of lower Hg-content food items in the littoral relative to profundal-benthic habitat. LNS is a bottom feeder whose diet consists of periphyton in juveniles and benthic invertebrates in larger adults (Brown and Graham 1954, Sayigh and Morin 1986, Scott and Crossman 1998). Adult stages are known to favor the deeper areas of lakes (Scott and Crossman 1998). Littoral-pelagic resource use quantified by the stable carbon isotope technique is thus likely to reflect littoral-profundal benthic dietary transitions in this species. This is because the carbon isotope signatures of pelagic and profundal-benthic

invertebrates tend to overlap in boreal lakes (Chapter 1, Vander Zander and Rasmussen 1999). Life-stage patterns of littoral-pelagic resource use and Hg accumulation also differed with community composition in this species. A negative relationship between LNS [Hg] and littoral resource use (Fig. 3-10), was mainly driven by a transition from littoral to profundal-benthic diet with increasing size and age in one lake (Ashuapamatikuan). In this case, a distinct community composition and physical ecosystem structure permitted greater reliance on profundal-benthic carbon by adult Long Nose Sucker, leading to greater Hg contamination. The effect of cross-habitat foraging on Hg accumulation in this species was thus also related to life-stage transitions in habitat use linked to lake features.

A distinction of horizontal littoral-pelagic resource use increased the explained variability in [Hg] among lakes in two out of three fish species (Northern Pike and Long Nose Sucker) (Fig. 3-11). Thus beyond spatial (littoral-pelagic) differences in Hg availability, our results demonstrated that species and life-stage differences in the type and size of prey consumed (and prey Hg contents) between littoral and pelagic habitats, affect Hg concentrations in fish in lake ecosystems. Quantifying the use of littoral versus pelagic carbon source by fish consumers is thus highly relevant to the evaluation of inter-specific and inter-system variations in the extent of Hg bioaccumulation.

Table 3-14. Summary of explained variability in [Hg] among lakes in each autecological type, based on the results of stepwise linear regressions and on factors identified in our discussion to explain the remaining variability in Hg levels.

	Quis type Northern Pike		Ubi type White Sucker	
		predictors		predictors
Variability in [Hg] explained by species–specific features	93.8%	FL(+), TrophP(+), $\%C_{LITT/PEL}$(+)	61.7%	Age(+)
Variability in [Hg] explained by both species AND lake-specific features	94.9%	FL(+), TrophP(+), $\%C_{LITT/PEL}$(+), [SPM](-), Age(+)	62.8%	Age(+), LArea(+)
Remaining variability	5.1%	- Among-lake differences in biological structure and available prey types affecting vertical resource utilization (i.e. onset of an ontogenetic trophic plateau). - Among-lake differences in Hg availability at the base of littoral and pelagic food webs. - analytical variability.	37.2%	– Among-lake differences in resource availability affecting bi-dimensional resource use and growth patterns. - Among-lake differences in Hg availability at the base of littoral and pelagic food webs. - analytical variability

Table 3-14 (continued)

			Aequivocus type LNS - community compositions			
	Aequivocus type LNS		Allopatric LNS		Sympatric LNS	
		predictors		predictors		predictors
Variability in [Hg] explained by species – specific features	77.1%	FL(+), Age(+)	87%	FL(+), Age(+),$\%C_{LITT/PEL}$(-)	76.5%	FL(+), Age(+),$\%C_{LITT/PEL}$(-)
Variability in [Hg] explained by species AND lake-specific features	78.5%	FL(+), Age(+), Darea(+)	0%		80.9%	FL(+), Age(+),$\%C_{LITT/PEL}$(-), Zmax(+)
	77.4%	FL(+), Community type(-)				
Remaining variability	≈22%		13%	- Lake-specific features affecting Hg availability and horizontal resource utilization. - analytical variability	19%	- Among-lake differences in physical structure affecting horizontal resource use and inter-specific interactions intensity. - Among-lake differences in Hg availability at the base of pelagic and littoral food webs. - analytical variability

Bi-dimensional feeding strategies determine biological and ecosystem effects on Hg bioaccumulation in fish.

Hg bioaccumulation in a Quis-type consumer

Northern Pike is a Quis-type consumer whose ontogeny determines metabolic requirements in terms of prey profitability and prey and habitat preferences. Resource exploitation across trophic levels and habitat boundaries tend to be similar among ecosystems in this autecological type, or vary in predictable manner with certain ecosystem features (Chapter 1). Hg exposure and uptake mediated by spatially explicit resource use should be similarly predictable in Northern Pike, following species-specific biological features and lake factors affecting its feeding behavior in two-dimensional space of lake ecosystems.

Vertical resource use by Northern Pike varied with size and age depending on lake. The occurrence of a trophic plateau in three lakes indicated that vertical resource utilization by Northern Pike eventually settles at a constant trophic level. The onset of this trophic plateau (i.e. exact size and age at which trophic position stabilizes) and average plateau trophic position differed among lakes. All Pikes had reached a trophic plateau around 600-650mm fork length in the study lakes. Northern Pike Hg concentrations increased linearly with body size and trophic position in a similar fashion among populations. Upon reaching of the trophic plateau however, trophic position no longer explained variations in Pike Hg concentrations. Instead, differences in Hg levels among lakes and individual fish were determined by horizontal littoral-pelagic resource use. Greater reliance on littoral prey was linked to greater Hg body burdens in adult life-stages, following lake-specific linear patterns. Littoral resource use was enhanced in lakes characterized by

larger perimeter to area ratios, a measure of littoral habitat dimensionality. Dimensionality favors prey aggregation and contributes to increase foraging success and yields in predatory species like Northern Pike (Whitehead and Walde 1992, Sass et al. 2006). Lake perimeter to area ratio also positively explained lake-specific patterns of Hg accumulation with Northern Pike age, perhaps as it affected horizontal cross-habitat prey choices. Biological factors and bi-dimensional feeding patterns thus explained nearly all variability (93.8%) in Northern Pike Hg levels among the study lakes. Consideration of lake SPM and NP age only slightly increased the predictive capacity of our linear model to 94.9%. Water column SPM was a negative predictor of NP Hg levels. Lower SPM concentrations likely indicated lower particulate Hg dilution and so potentially greater Hg bioavailability at the food web base. Our model suggests that larger and older Pike feeding on higher trophic level littoral prey in oligotrophic lakes characterized by low suspended particulate matter concentrations, may reach higher Hg levels in boreal lakes. Table 3-14 summarizes the explained variability in Hg concentrations in Quis-type Northern Pike, distinguishing between species and ecosystem specific influences. Similar bi-dimensional resource use and dietary pathways for Hg assimilation in Northern Pike reflected consistent life-history strategies among lakes that varied in predictable manner with certain lake features. As a result, changes in vertical and horizontal resource use directly affecting Hg uptake, encompassed ecosystem-specific influences on Hg exposure and availability. This limited among-lake differences in the extent of Hg bioaccumulation in this species, and made Northern Pike Hg levels highly predictable. We suggest that predictable bioaccumulation patterns among ecosystems is a general characteristic of

Quis-type consumers, providing ecosystem features affecting their bi-dimensional feeding ecologies have been identified.

Hg bioaccumulation in an Ubi-type consumer

White Sucker is an Ubi-type consumer whose ontogeny establishes a range of exploitable resources (mainly by determining feeding capacities), but whose feeding patterns are otherwise determined by lake features affecting resource availability and prey abundance (Chapter 1). Bi-dimensional resource utilization determined by ecosystem characteristics therefore tends to be highly variable within and among ecosystems in this autecological type. Hg exposure and uptake via spatially explicit resource use should be similarly variable in White Sucker, and limit the explanation of among-lake differences in Hg concentrations.

White Sucker was only sampled in the three lakes and was characterized by different growth rates in these systems. Among-lake differences in growth underlined the variable character of the species feeding ecology. Vertical trophic position increased with body size but was highly variable in ≥400mm individuals, indicating important trophic omnivory in adult stages. Trophic position varied negatively with littoral resource use, suggesting that White Sucker fed at lower trophic levels in the littoral relative to pelagic habitat in the study lakes. Littoral resource use was enhanced by water transparency and larger drainage areas, two distinctive characteristics of Enakapeshakamau Lake. While this was not observed in the study lakes, secchi depth and drainage area likely stimulate littoral periphyton productivity (i.e. via greater nutrient inputs from larger watersheds and greater light penetration (Desrosiers et al. 2006a and 2006b)). Littoral-pelagic resource use explained the lake-specific character of Hg–fork length relationships in White Sucker.

A distinct pattern of Hg accumulation with body size was observed in Enakapeshakamau Lake where the species mainly relied on littoral dietary items. White Sucker growth also differed in Enakapeshakamau relative to other lakes. Variable growth rates resulting from changes in diet can affect Hg uptake by fish (MacCrimmon et al. 1983). In Enakapeshakamau Lake, a different growth rate and enhanced littoral resource use affected Hg accumulation by White Sucker. Under the age of ten, WS were comparatively smaller, relied more upon littoral resources and reached higher Hg levels (in the average-size class (scII)) in Enakapeshakamau relative to other lakes. Thus while age was the only significant predictor of White Sucker Hg in the study lakes (based on stepwise linear regressions), the age effect was not independent from ecosystem-specific differences in growth and littoral-pelagic resource use likely affecting Hg exposure and uptake by White Sucker. Nonlinear ecosystem influences affecting bi-dimensional resource use and growth patterns explain that species-specific biological features like fork length and age only accounted for 47% and 62% of the variability in White Sucker Hg levels among lakes. We suggest that such a weak influence of biological features on bioaccumulation patterns is a distinctive trait of Ubi-type consumers. Table 3-14 summarizes the explained variability in Hg concentrations in Ubi-type White Sucker. Our results illustrate the variable and opportunistic feeding ecology that characterizes this autecological type, and the corresponding difficulty to predict inter-system variations in Hg concentrations in Ubi species. Our assessment of ecosystem influences was however limited by a small lake sample number. In consequence, we anticipate that greater predictability in Ubi-type fish Hg concentrations could be achieved by considering larger

sample number and by focusing the analysis on lake features affecting resource availability and prey abundance in two-dimensional space of aquatic ecosystems.

Hg bioaccumulation in an Aequivocus consumer

Long Nose Sucker is an Aequivocus type consumer characterized by ontogenetic habitat and dietary preferences. Such life-history specialization makes Aequivocus consumers highly sensitive to resource exploitation under community interactions. Bi-dimensional resource use is thus equally determined by species-specific ontogeny, community composition and physical ecosystem structure in this autecological type (Chapter 1). Spatially-explicit dietary pathways for Hg bioaccumulation in Long Nose Sucker, should follow similar patterns among ecosystems with analogous community composition and vary in predictable manner with physical ecosystem structure and preferred habitat dimensionality.

Littoral-pelagic resource use varied negatively with fork length and age in Long Nose Sucker. This indicated the strength of life-history effects on cross-habitat foraging in this species. Linear patterns of decreasing littoral resource use with increasing size and age were driven by life-stage transitions of littoral-profundal benthic resource use linked to physical ecosystem structure and a distinct community composition in one lake. Important depth, the absence of a benthic competitor (in White Sucker) and lower predation risk from Northern Pike in Ashuapamatikuan Lake, permitted greater reliance on littoral carbon in juveniles and greater reliance on profundal-benthic carbon in larger adults Long Nose Sucker (Chapter 1). This in turn was linked to greater Hg concentrations in all life-stages of Long Nose Sucker in this lake, and a distinction of Hg accumulation patterns with age between community types. Aside from life-stage patterns

of littoral-pelagic resource use, greater Hg exposure for Long Nose Sucker in Ashuapamatikuan Lake may have been related to its lower primary productivity and extensive drainage area. Primary production favors Hg biodilution at the base of lake food webs, thereby lowering Hg intake in fish consumers (Meili 1991, Kidd et al. 1999, Chen et al. 2005). Drainage area is proportional to Hg influx to lakes from their surrounding watersheds (Desrosiers et al. 2006a). Fork length and community composition still explained a similar amount of variability (77.4%) in Long Nose Sucker Hg than FL, age and lake drainage area combined (78.5%). Allopatric Long Nose Sucker in Ashuapamatikuan Lake accumulated more Hg than sympatric populations of the Eagle river watershed. Among sympatric populations, Hg concentrations were also negatively related to littoral resource use and varied positively with lake depth. This indicated similar ontogenetic transitions towards more contaminated profundal-benthic prey with increasing size and age in adult stages, as permitted by the physical extent of the profundal-benthic habitat. Deeper lakes also potentially alleviated inter-specific interactions intensity in sympatric populations, permitting greater reliance on preferred (and higher Hg content) food items in larger adults. Our linear models indicated that larger and older Long Nose Sucker reached higher Hg concentrations in deeper boreal lakes where it relied more upon profundal-benthic dietary items, depending on community composition. Table 3-14 summarizes the explained variability in Hg concentrations in Aequivocus-type Long Nose Sucker, distinguishing between species and ecosystem specific influences as well as community types. Our analysis demonstrated the concomitant influence of biological and ecosystem factors for determining Hg levels in Aequivocus consumers. A difference in community composition and physical

ecosystem structure affecting life-history strategies of horizontal resource use in Long Nose Sucker, also affected Hg exposure and uptake by the species among lake ecosystems. This permitted to identify important linkages between species and ecosystem determinants of Hg bioaccumulation. The prediction of Hg levels in Aequivocus consumers must thus take into account differences in community type and preferred habitat dimensionality, as this affects horizontal dietary patterns of Hg uptake with biological traits in Aequivocus species.

CONCLUSIONS AND IMPLICATIONS

A bi-dimensional approach to the feeding ecology of fish integrates spatial effects on Hg exposure, assimilation and trophic transfers. Our study showed that littoral-pelagic differences in the type and size of prey consumed between littoral and pelagic habitats in lake ecosystems, affect Hg exposure and uptake by fish consumers. It may also complement the influence of trophic position for determining the extent of Hg biomagnification in some species. Classified by autecological types, bi-dimensional feeding strategies further provide species-specific distinctions for the relative importance of biological versus environmental determinants of Hg bioaccumulation. Distinguishing consumers by autecological type can facilitate the evaluation of fish Hg concentrations among lake ecosystems or in response to changing ecosystem conditions. Based on our observations, we can speculate that modifications to Hg inputs to lake ecosystems would have a direct effect on Hg concentrations in Quis-type consumers, that habitat modifications affecting community interactions would similarly affect Hg levels in Aequivocus consumers, and that any changes in system productivity, prey abundance and

resource availability (due to climate change, eutrophication, etc), will alter Hg bioaccumulation in Ubi consumers. The quantification of bi-dimensional, spatially-explicit feeding patterns in fish, permits to identify important linkages between species and ecosystem effects on Hg dietary pathways, and should improve our ability to generalize predicted consequences of Hg management strategies and policies.

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4. CHapter 4

CAN BI-DIMENSIONAL FOOD WEB STRUCTURE ACCOUNT FOR SPATIAL VARIATIONS IN THE EXTENT OF MERCURY BIOACCUMULATION IN FISH ACROSS BOREAL AQUATIC ECOSYSTEMS?

ABSTRACT

Natural lakes and hydroelectric reservoirs serve subsistence fishing activities in aboriginal communities throughout the Canadian boreal forest. Mercury (Hg) concentrations in fish from boreal aquatic ecosystems often exceed the advisory limit of 0.5ppm for safe human consumption in piscivorous species. Hg contamination management remains complicated by spatial variations in fish Hg levels among lake ecosystems receiving comparable Hg inputs, and by the retention of elevated Hg levels in fish from hydroelectric reservoirs more than 30 years after impoundment. Bi-dimensional food web structure integrates horizontal contributions from spatially-distinct carbon source to the vertical trophic organization of biological communities. Here we contrast bi-dimensional food web structures and fish Hg contamination in pristine natural lakes and a reservoir ecosystem controlled by anthropogenic activities. We suggest that bi-dimensional food web structures determine trophic and spatially-explicit dietary pathways for Hg uptake by fish in aquatic environments, and as such can improve predictions of fish Hg concentrations among systems. We use variations in stable isotope ratios of nitrogen and carbon to characterize spatially-explicit resource exploitation in fish communities and bi-dimensional food web structures. Horizontal spatial processes here distinguish between allochthonous-autochthonous carbon source contributions to primary producer-consumer at the food web base, and between littoral and pelagic carbon source contributions in fish consumers. Our results demonstrate (i) that greater incorporation of autochthonous-respired carbon by primary producers leads to greater Hg bioaccumulation in fish and contribute to explain the retention of elevated fish Hg levels in a reservoir relative to nearby lakes; (ii) that littoral dietary pathways enhance Hg exposure and uptake by fish in aquatic ecosystems and (iii) that bi-dimensional food web structures estimated from average trophic position and littoral-pelagic resource use in fish communities, or from physical and biological ecosystem characteristics affecting bi-dimensional resource use by fish, can facilitate and improve predictions of fish Hg concentrations among boreal aquatic ecosystems.

INTRODUCTION

Mercury (Hg) concentrations in fish from boreal aquatic ecosystems commonly exceed the advisory limit of 0.5ppm for human consumption in piscivorous species (Lindqvist et al. 1991, Bodaly et al. 1993, Schetagne et al. 1999, Kamman et al. 2005). Natural geological sources are contributors of Hg to boreal shield environments (Rasmussen 1994, Rasmussen et al. 1998). Yet long-range atmospheric transport and deposition of anthropogenic Hg sources mainly account for elevated Hg levels in boreal ecosystems remote from human activities and point sources of Hg emissions (Lindqvist et al. 1991, Jackson 1997, Fitzgerald et al. 1998, Wang et al. 2004). In Canada, human exposure to Hg through fish consumption remains a public health concern, especially for remote communities relying on subsistence fisheries. Both natural lakes and hydroelectric reservoirs serve subsistence fishing purposes in aboriginal communities throughout the Canadian boreal forest. In natural lakes, Hg management remains complicated by spatial variations in Hg contamination among ecosystems receiving comparable Hg inputs. Hence Hg concentrations in a given fish species of a given size and age, tend to vary greatly among lakes (Lindqvist et al. 1991, Bodaly et al. 1993, Braune et al. 1999, Schetagne et al. 1999, Kamman et al. 2005). In reservoir ecosystems, Hg contamination of fish is accentuated by the release of organic matter and soil-bound inorganic Hg during the flooding of organic-rich soils and terrestrial vegetation (Jackson 1988, Jackson 1991, Tremblay and Lucotte 1997, Mailman et al. 2006). Abundant organic matter stimulates microbial processes including mercury methylation, thus increasing Hg bioavailability to reservoir biota (Jackson 1988, Mailman et al. 2006). This leads to rapid increases in fish Hg concentrations following impoundment (Johnston et al. 1991), that may persist for up

to 30 years in some reservoirs (Mailman et al. 2006). Several factors contribute to maintain elevated Hg levels in reservoir fish and are known to cause inter-system variations in fish Hg levels among natural lakes. These include ecosystem-specific factors affecting Hg bioavailability and trophic transfers, and species-specific factors influencing Hg assimilation and bioaccumulation (see Chapter 3). Numerous studies have identified these factors and described their respective role in Hg biogeochemical pathways. Yet knowledge of common actions and implications for both environmental (system-specific) and biological (species-specific) determinants of Hg levels fish is still lacking. This continues to prejudice our ability to predict Hg concentrations in fish, and thus human exposure, even on a regional basis.

Recently, bi-dimensional feeding ecologies that link feeding patterns, life-history traits and ecosystem attributes, were shown to facilitate the evaluation of inter-system variations in fish Hg levels by species (Chapter 3). Together, horizontal (spatially-explicit) and vertical (trophic) resource exploitation determine dietary pathways for Hg uptake by fish in two-dimensional space of aquatic ecosystems (Chapter 3). A similar distinction of horizontal spatially distinct carbon source-flux at the food web level may equally facilitate the evaluation of inter-system differences in Hg levels among fish communities. Bi-dimensional food web structure integrates horizontal spatially distinct carbon source contributions to the vertical trophic organization and dynamics of consumer communities (Chapter 2). In lake food webs, horizontal spatial processes distinguish between autochthonous-allochthonous carbon source contributions to primary consumers, and between littoral and pelagic carbon source contributions to secondary and tertiary consumers (Fig. 4-1). Both carbon source-flux pathways have been shown to

influence Hg bioaccumulation. Higher levels of autochthonous carbon (as microalgae and bacteria) in the fine particulate matter of reservoir ecosystems, was linked to greater Hg bioavailability and transfers to lower food webs (Montgomery et al. 2000). Littoral-pelagic resource use by fish consumers affects their Hg concentrations (Power et al. 2002a, Gorski et al. 2003, Chapter 3). This influence is variable depending on inter-system differences in Hg availability at the base of littoral and pelagic habitats, and inter-specific differences in the type and size of prey consumed across habitat boundaries.

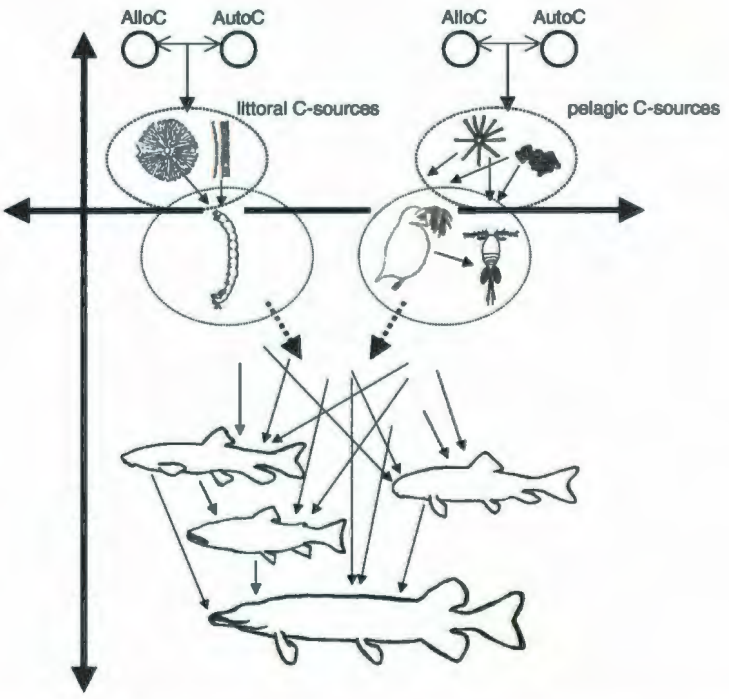

Fig. 4-1. Schematized bi-dimensional food web structure of aquatic ecosystems, integrating horizontal carbon source-flux to vertical trophic organization. Horizontal spatial processes distinguish between allochthonous (AlloC) and autochthonous (AutoC) carbon source contributions at the food web base, and between littoral and pelagic carbon source (C-source) contributions to fish consumers.

Here we demonstrate the application of a bi-dimensional approach to food web structure to explain differences in Hg bioaccumulation in fish among natural lakes and between natural lakes and a reservoir ecosystem, more than 33 years after impoundment. We use

variations in stable isotope ratios of carbon and nitrogen to quantify bi-dimensional food web structures as horizontal reliance on littoral-pelagic carbon and vertical trophic position in fish communities. Stable carbon isotopes are also used to evaluate the importance of autochthonous-allochthonous carbon source contributions at the base of food webs. Autochthonous contributions here refer to the incorporation of *in-situ* recycled carbon by primary producer/consumer. As a site-specific feature related to consumer ontogeny and ecosystem characteristics, bi-dimensional food web structure should facilitate the evaluation of inter-system differences in Hg bioaccumulation in fish, and permit to improve the management of Hg contamination and human exposure.

MATERIAL AND METHODS

This study was undertaken as part of the Labrador component of the "Mercury in Lakes of the Boreal Forest Ecosystem" research initiative within the Canadian Collaborative Mercury Research Network (COMERN). Study sites were selected and sampled in partnership with the Labrador Innu, based on their relative importance to Innu subsistence fishing activities and harvest.

Study sites - Natural Lakes

Five pristine boreal lakes remote from human settlements and developments such as roads were selected for analysis (Fig. 4-2A). All lakes were oligotrophic, supported relatively simple biological communities and differed in size and morphometry (Table 4-1).

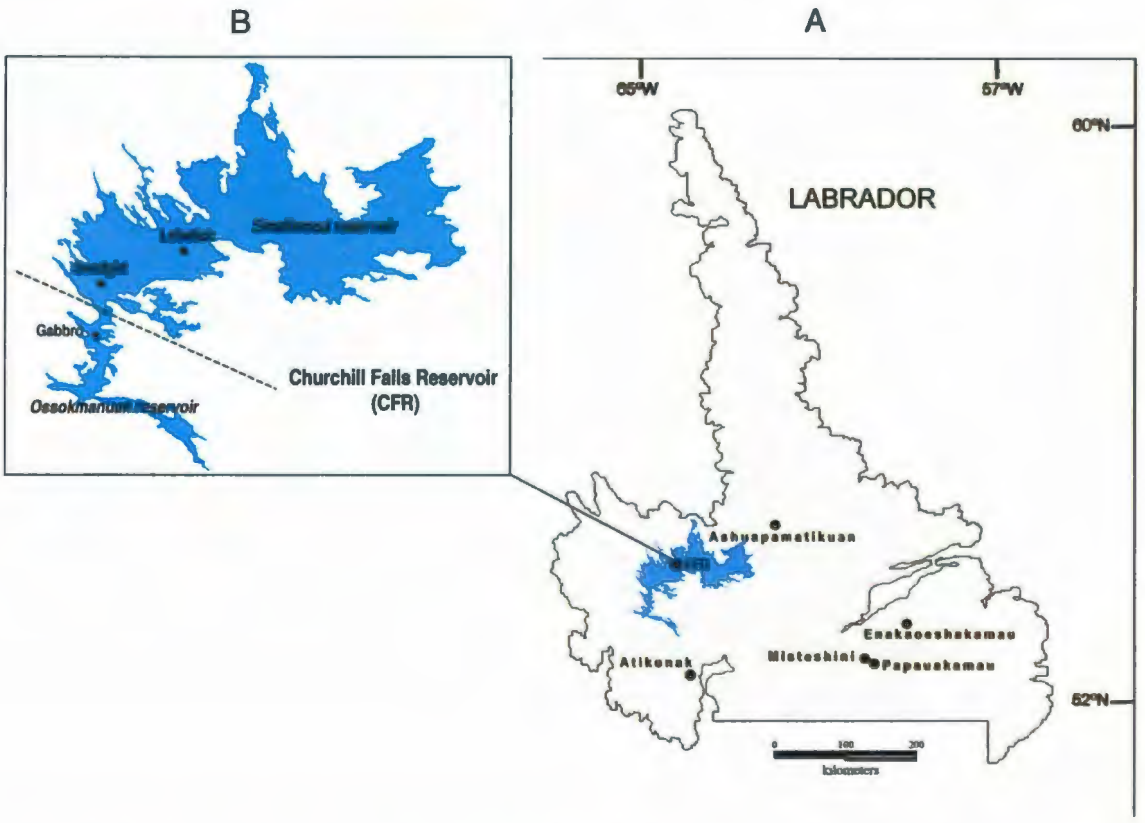

Fig. 4-2. (A) Map of Labrador showing the study sites. (B) Enlargement of the Churchill Falls Reservoir (CFR) showing sub-divisions between Ossokmanuan and Smallwood reservoirs (separated by the dash line) and location of sampling stations.

Labrador is characterized by a cold continental climate with mean annual temperatures of -1.2°C. Total annual precipitation average 975mm, with annual means of 542mm and 471cm falling as rain and snow, respectively (Environment Canada 2004b). The region is typically under snow cover from late October until late May to early June, during which time lakes are ice covered. Riparian vegetation at all sites was dominated by black spruce (*Picea mariana*), in some areas associated with balsam fir (*Abies balsamea*). Igneous rock surfaces characterize the easternmost Canadian Shield region and exposed precambrian granite is the dominant feature of Labrador bedrock geology (Sutton 1972).

Study sites- Reservoir

The Churchill Falls Reservoir (CFR) is located on the central-western Labrador plateau and is at the head of the Churchill Falls hydroelectric power development. The CFR comprises two interconnected reservoirs: the Ossokmanuan reservoir formed by the flooding of Gabbro and Ossokmanuan lakes in 1961, and the Smallwood Reservoir created by the flooding of five lakes (Sandgirt, Lobstick, Michikamau, Orma and Adelaide) in 1971. The original lakes are now separated by narrow channels, control structures, or submerged trees. Approximately 2,300km^2 of low bogland and spruce forest were flooded upon filling of the CFR (Newfoundland and Labrador Hydro, personal communications). As opposed to a single large dam, water is contained in the CFR by a series of 88 dykes totaling 64.4km in length. The reservoir has a total surface area of 7,269km^2 and a storage volume of 31.1billion cubic meters (CF(L)Co 2004). In spite of fish consumption advisories for elevated Hg levels in piscivorous species (Environment Canada 2004a), the Labrador Innu continue to engage in subsistence fishing in the CFR, and sampling sites were selected accordingly. Three CFR sites were selected for sampling: Gabbro, Lobstick and Sandgirt (based on the original lake names of currently flooded sections) (Fig. 4-2B). The Gabbro station is part of the older Ossokmanuan reservoir that flows into the Smallwood reservoir via the Gabbro control structure. Sandgirt and Lobstick stations form a single basin within the Smallwood reservoir. The CFR is characterized by an annual draw-down cycle where the Ossokmanuan reservoir is emptied into the Smallwood reservoir through spring, and is refilled by October. The Smallwood Reservoir is filled by summer or early fall, and undergoes over-winter draw-

down depending on yearly energy demands (Newfoundland and Labrador Hydro, personal communications).

Field sampling

Lakes were accessed by floatplane or helicopter and sampled during the summers of 2002 and 2003 or 2004. Reservoir sites were accessed via dyke maintenance roads and sampled during the summer of 2004. pH and Secchi depths were measured on-site for natural lakes and all lakes were sampled for pelagic chlorophyll-*a* (Chla) determination. pH and Chla values for reservoir sites were provided by Newfoundland and Labrador Hydro (2000). Single measures were provided for the basin comprising Lobstick and Sandgirt stations in the reservoir. All sites (lakes and reservoir stations) were individually sampled for fish, plankton, suspended particulate, periphyton, and for aqueous, particulate and periphyton total Hg determination. Sampling methods are described in detail in Chapter 3. Two distinct water column and periphyton sampling stations were used in natural lakes, as opposed to a single one in each reservoir station. Lakes and reservoir sites were physically characterized using GIS for surface area (Area) and perimeter (Peri). Common area and perimeter values were determined for the basin comprising Lobstick and Sandgirt stations within the reservoir.

Laboratory analysis

Suspended particulate matter (SPM) concentrations were measured as dry weights. Periphyton biomass (Biomass(peri)) was estimated as ash free dry weight (AFDW). Chla concentrations were measured as fluorescence after overnight extraction in 90% acetone at 4°C and in the dark. PAratio is the ratio of lake perimeter over lake surface area.

Shoreline development index (SDI) measures lake shape as its degree of irregularity relative to a perfect circle and is calculated as: $SDI = LPeri/(2*\sqrt{(LArea*\pi)}$.

Stable isotope analysis

Stable isotope ratios of carbon and nitrogen were separately determined for lyophilized fish tissue (white muscle) samples (n=293) and plankton size-fractions (≥53, 100, 200 and 500μm) (n=48) on a stable isotope ratio mass spectrometer (Finnigan, MAT252). Plankton samples were homogenized using a glass rod prior to stable isotope analysis. Fish samples were homogenized using an agate mortar and pestle. The carbon isotopic composition of periphyton (n=29) and SPM (n=13) filter samples were measured on a different mass spectrometry system (GV instruments, Isoprime). Plankton samples analyzed on both systems yielded similar isotopic ratios within ±0.18‰ for $\delta^{13}C$, and ±0.27‰ for $\delta^{15}N$. Stable isotopic compositions are measured as the ratio of the heavier to the lighter isotope of an element and expressed as permil difference (delta notation (δ)) from the same ratio in a standard reference material (i.e. $\delta^{13}C_{fish} = [((^{13}C/^{12}C)_{fish} / (^{13}C/^{12}C)_{VPDB}) - 1] *10^3$). Values are reported relating to international standards: Vienna Pee Dee belemnite (VPDB) limestone for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$. The isotopic composition of a replicate fish tissue sample included in all analysis was equivalent to ±0.11‰ for $\delta^{13}C$ and ±0.09‰ for $\delta^{15}N$.

Mercury analysis

Aqueous Hg ($[Hg]_{aq}$) and total Hg determinations for SPM ($[Hg]_{SPM}$) and periphyton ($[Hg]_{peri}$) samples, were conducted by atomic fluorescence following the method of Pichet et al. (1999). Detection limits for $[Hg]_{aq}$ was $0.2 ngL^{-1}$. Total Hg concentrations [Hg] were

determined for lyophilized fish muscle tissue (n=293) by isotope dilution on a Perkin Elmer ELAN 6100 ICP-MS equipped with a FIAS 400 system. Nearly all (≈99%) Hg in fish muscle tissue is in the form of MeHg (Bloom 1992). Samples were digested by heating spiked (^{201}Hg enriched) samples to 60°C overnight with concentrated HNO_3. HNO_3 was added the following day and samples were digested for 2 more hours. H_2O_2 was added to complete the digestion process. BrCl was added to oxidize all forms of mercury to Hg^{2+}. After 12 hours, the un-reacted BrCl was neutralized by addition of NH_2OH HCl. Samples were then diluted and mercury was reduced from Hg^{2+} to Hg^0 by on-line addition of $NaBH_4$ to generate Hg vapor. The ratio of net counts of ^{202}Hg to ^{201}Hg was used to determine total Hg. QA/QC (μg/g dry wt.) for DORM-2 = 4.64/4.04, for DOLT-2 = 2.14/2.07. Mean concentration for method blanks was 0.00009 μg/g.

Fish communities

Seven different fish species were collected across the study lakes and reservoir stations: Brook Trout (*Salvelinus fontinalis* (Mitchill), Lake Trout (*Salvelinus namaycush* (Walbaum)), Long Nose Sucker (*Catastomus catostomus* (Forster)), Northern Pike (*Esox lucius* (Linnaeus)), Ouananiche, (*Salmo salar* (Linnaeus)), White Fish (*Coregonus clupeaformis* (Mitchill)), and White Sucker (*Catastomus commersoni* (Lacépède)). These species were not represented in every site, and varied in numbers and body size when present. For this reason, individual species were size-structured for analysis. Three size classes were *a priori* defined for each species based on biological data (Scott and Crossman 1998) and Hg bioaccumulation trends outlined in earlier Labrador Hg studies (Bruce et al. 1979, Scruton 1984). Size class I (scI) comprised juvenile fish (≤2 years

old), scII contained average size adults, and scIII contained larger-than-average size adults. This size structure was shown to be useful in accounting for individual species ontogenetic transitions in bi-dimensional resource exploitation (Chapter 1). Sample numbers were limited to a maximum of 5 specimens per size class in each species, up to a maximum of 15 fish per species per site. Resulting community composition and sample sizes are shown in Table 4-2. For statistical analysis, community composition was used as a dummy variable to distinguishing fish communities having only Northern Pike as a top predator (community type=0) from fish communities having Lake Trout as another top predator and a pelagic-benthic forage species in White Fish (community type=1) (Table 4-2).

Stable isotope data

Autochthonous-allochthonous carbon source distinction at the base of food webs

The carbon isotopic compositions of periphyton, SPM and different plankton size-fractions were used to qualitatively assess the contributions of autochthonous versus allochthonous carbon source to lower food webs. In boreal ecosystems such as those considered in this study, food web production is mainly sustained by carbon of allochthonous origin (France 1997, Wetzel 2001, Carpenter et al. 2005). Rather uniform $\delta^{13}C$ values of –26‰ to –28‰ characterize allochthonous carbon derived from terrestrial vegetation (Hecky and Hesslein 1995, France 1997, Grey et al. 2000) and terrestrial soils (Karlsson et al. 2003) in boreal environments. Autochthonous contributions in this case refer to *in-situ* recycled (or respired) carbon of allochthonous origin, which will have

lighter $\delta^{13}C$ signatures (Rau 1978, del Giorgio and France 1996, France and Schlaepfer 2000).

Bi-dimensional food web structures

The carbon isotopic compositions of periphyton and SPM+53μm-plankton were used as site-specific littoral and pelagic isotopic endpoints ($\delta^{13}C_{littoral}$ and $\delta^{13}C_{pelagic}$) to estimate horizontal reliance on littoral versus pelagic carbon source by fish: $\%C_{LITT/PEL} = [(\delta^{13}C_{fish} - \delta^{13}C_{pelagic})/ (\delta^{13}C_{littoral} - \delta^{13}C_{pelagic})] * 100$ (Fry and Sherr 1984). This mixing model assumes no trophic fractionation of carbon isotopes, as this was shown to correlate well with stomach contents estimates of zoobenthivory in fish from north-temperate lakes (Vander Zanden and Vadeboncoeur 2002). The isotopic signatures of SPM and the 53μm plankton fraction were combined to yield a pelagic baseline composition and trophic position similar to that of littoral periphyton, which necessarily contains both primary producers and microbial consumers. In all sites, littoral periphyton was enriched in ^{13}C and thus distinguishable from pelagic SPM and 53μm-plankton $\delta^{13}C$, due to boundary layer effects on carbon availability and fractionation by primary producers during photosynthesis (France 1995, Hecky and Hesslein 1995). Horizontal food web structure was estimated as average littoral-pelagic resource use ($\%C_{LITT/PEL}$) in fish consumers, weighted by species and size class (following the equation developed in Chapter 2). Community mean values of fish $\%C_{LITT/PEL}$ were also used for statistical comparisons. Nitrogen isotopic compositions of 53μm-plankton were used as site-specific nitrogen isotopic baselines ($\delta^{15}N_{baseline}$) to estimate fish vertical trophic position: $TrophP = \lambda + (\delta^{15}N_{fish} - \delta^{15}N_{baseline}) / \Delta^{15}N$ (where λ is the trophic position of baseline organisms (=1)

and $\Delta^{15}N$ is equivalent to +3.4‰) (Post 2002a). For each site, vertical food web structure was estimated as the average trophic position (TrophP) of all fish consumers weighted by species and size class (using the equation developed in Chapter 2). Community mean values of fish TrophP were also used for statistical comparisons. Values of site-specific isotopic baselines and endpoints are shown in Table 4-3. Estimates of vertical and horizontal food web structure are presented in Table 4-4. Site-specific bi-dimensional food web structures are depicted on two orthogonal axes in Fig. 4-8.

Table 4-1. Physico-chemical and biological characteristics of the study sites, with fish communities composition and baseline (aqueous, particulate and periphyton) total Hg concentrations (mean values).

	Natural lakes					Reservoir stations		
	Ashua	**Atik**	**Enaka**	**Mista**	**Papaua**	**Gabbro**	**Lobstick**	**Sandgirt**
Coordinates	54°39'N 62°24'W	52°38'N 64°33'W	53°15'N 59°04'W	52°46'N 59°35'W	52°41'N 59°24'W	53°37'N 65°15'W	53°59'N 64°47'W	53°53'N 65°14'W
Area (km^2)	17.21	456	20.65	6.21	27.43	859	2060	2060
Peri (km)	27.25	1278	54.43	10.15	43.94	1914	3332	3332
PA ratio	1.61	2.80	2.64	1.64	1.60	2.23	1.62	1.62
SDI	1.9	16.9	3.4	1.1	2.4	18.4	20.7	20.7
pH	6.3	7.0	6	5.9	5.8	6.9	7.1	7.1
Secchi (m)	5	3.1	7	1.5	2	3.5	2.5	2.3
SPM (mg/L)	0.14	0.71	0.21	0.93	1.55	0.74	1.62	0.92
Chla (µg/L)	0.67	1.47	0.82	1.94	2.68	1.70	1.43	1.43
Biomass(pp) (µg/cm^2)	1492	952	610	2464	1567	1695	381	330
[Hg](aq) (ng/L)	2.16	1.035	2.23	2.75	2.84	0.84	0.55	0.925
[Hg](pp) (ng/g)	5	139	113	184	19	75	250	213
[Hg](SPM) (ng/g)	407	240	581	166	348	184	314	363
Fish community	LNS, LT, NP, WF	LNS, LT, NP, WF, WS, Ssp.	BT, LNS, NP, WS, SS	BT, LNS, NP, WS	BT, LNS, NP, WS	LNS, LT, NP, WF, WS, Ssp.	LNS, LT, NP, WF, WS, Ssp.	LNS, LT, NP, WF, WS

Ashua=Ashuapamatikuan Lake, Atik=Atikonak Lake, Enaka=Enakapeshakamau Lake, Mista= Mistashini Lake, Papaua= Papauakamau Lake. Fish communities: BT= Brook Trout (S. fontinalis), LNS=Long Nose Sucker (C.catostomus), LT=Lake Trout (S. namaycush), NP=Northern Pike (E. Lucius), WF=White Fish (C. Clupeaformis), WS=White Sucker (C. commersoni), SS= Ouananiche (S. salar), Ssp= Sucker sp. (fish from the genus Catostomus that could not be identified to species). Peri=perimeter. PAratio= ratio of perimeter/area. SDI=shoreline development index. SPM=suspended particulate matter. Chla=chlorophyll-*a*. Biomass(pp)=periphyton biomass. [Hg]=total mercury concentrations. (aq)=aqueous. (pp)=periphyton. (SPM) suspended particulate.

Table 4-2. Sampled fish community composition by study sites. Sample sizes by species, populations (pop) and size classes (sc) for (A) natural lakes and (B) reservoir stations. scI= juvenile fish (≤age 2+), scII=average-size fish, scIII=larger adults.

(A)

	Ashuapamatikuan				Atikonak				Enakapeshakamau				Mistashini				Papauakamau			
Fish species	pop	scI	scII	scIII	pop	scI	scII	scIII	pop	scI	scII	scIII	pop	scI	scII	scIII	pop	scI	scII	scIII
BT	0				0				12	2	5	5	5			5	3			3
LNS	13	4	4	5	8	5	1	2	10		5	5	11	3	3	5	9	3	2	4
LT	10		5	5	5			5	0				0				0			
NP	11	1	5	5	13	1	7	5	5	1	3	1	15	5	5	5	8		3	5
WF	14	5	4	5	12	5	2	5	0				0				0			
WS	0				1			1	10		5	5	11	1	5	5	7		2	5
SS	0				0				5	5			0				0			
Ssp.	0				3		3		0				0				0			
Community totals	**48**	**10**	**18**	**20**	**42**	**11**	**13**	**18**	**42**	**8**	**18**	**16**	**42**	**9**	**13**	**20**	**27**	**3**	**7**	**17**
Community type	**1**				**1**				**0**				**0**				**0**			

(B)

	Gabbro				Lobstick				Sandgirt			
Fish species	pop	scI	scII	scIII	pop	scI	scII	scIII	pop	scI	scII	scIII
BT	0				0				0			
LNS	3			3	6		1	5	6		1	5
LT	3		2	1	1			1	3		1	2
NP	11	1	5	5	9		5	4	7		5	2
WF	5			5	9		4	5	15	5	5	5
WS	1		1		5			5	1			1
SS	0				0				0			
Ssp.	2	1	1		5	5			0			
Community totals	**25**	**2**	**9**	**14**	**35**	**5**	**10**	**20**	**32**	**5**	**12**	**15**
Community type	**1**				**1**				**1**			

See Legend in Table 4-1 for fish species identification

Table 4-3. Values of site-specific isotopic baselines and endpoints (means ± SE) used to estimate vertical TrophP (δ^{15}N-baselines) and horizontal $\%C_{LITT/PEL}$ (δ^{13}C-endpoints) in fish. T-tests results demonstrate statistically significant differences between littoral-pelagic δ^{13}C-enpoints in every sites.

		δ^{15}N-baselines		δ^{13}C-endpoints						
		(53µm-plankton)		littoral (periphyton)		pelagic (SPM+53µm)		t-tests		
		n	δ^{15}N	n	δ^{13}C	n	δ^{13}C	t	df	p-value
natural lakes	Ashua	2	2.7±0.5	4	-23.4±0.2	4	-27.3±0.9	-4.35	6	0.005
	Atik	2	2.0±0.1	4	-23.9±0.4	4	-30.1±0.3	-12.03	6	<0.001
	Enaka	1	2.0	4	-22.4±1.1	3	-27.8±0.6	-5.59	5	0.003
	Mista	2	2.1±0.1	4	-18.8±0.9	4	-27.9±0.5	-13.44	6	<0.001
	Papaua	1	0.4	4	-19.6±0.4	4	-28.7±0.3	-17.99	6	<0.001
CFR stations	Gabbro	1	3.3	3	-23.4±0.1	2	-29.6±0.03	-32.85	3	<0.001
	Lobstick	1	2.9	3	-25.7±0.2	2	29.6±0.5	-8,81	3	0.003
	Sandgirt	1	3.2	3	-24.1±0.2	2	29.9±0.3	-15.18	3	0.001

Data analysis

Differences in aqueous, periphyton and particulate total Hg concentrations between natural lakes and reservoir stations were assessed using t-tests. Periphyton, SPM and plankton δ^{13}C were compared between natural lakes and reservoir stations and among natural lakes only using t-tests and one-way ANOVA. Linear regressions were used to test whether carbon isotopic compositions of littoral (periphyton) and pelagic (SPM+53µm-plankton) isotopic endpoints were related to Hg concentrations in fish. Biological, mercury, stable isotope data and estimates of bi-dimensional food web structure are summarized by fish community in Table 4-4. Average fish fork length, age, Hg concentrations, TrophP and $\%C_{LITT/PEL}$ were compared among natural lakes, reservoir stations, and between natural lakes and reservoir stations using one way ANOVA and t-tests. In ANOVA, pairwise comparisons were conducted using Tukey's HSD test. For each site, community Hg was estimated by weighing fish Hg concentrations by species and size class using the following equation:

$$\text{Community Hg} = \underset{\text{specie \#1}}{((\Sigma[Hg]/n^{sc})/(n^{t}/n^{s}))} + \underset{\text{specie \#2}}{((\Sigma[Hg]/n^{sc})/(n^{t}/n^{s}))} + \underset{\text{specie \#3}}{((\Sigma[Hg]/n^{sc})/(n^{t}/n^{s}))} + \underset{\text{specie \#4}}{((\Sigma[Hg]/n^{sc})/(n^{t}/n^{s}))}$$

Where:

[Hg]	= individual fish Hg concentration
n^{sc}	= number of size classes per species (=3)
n^{t}	= total number of fish sampled in a site
n^{s}	= number of different species sampled in a site

Fish Hg concentrations were also compared by species among lakes and between natural lakes and reservoir stations. GLM procedure was used to differentiate Hg accumulation patterns with fish fork length, age, TrophP and $\%C_{LITT/PEL}$ among lakes, among reservoir stations, and between natural lakes and reservoir stations. Fish Hg data was log-transformed (base 10) in order to reduce residuals heteroscedasticity. Correlations between site-specific characteristics and estimates of horizontal or vertical food web structure were conducted using Pearson correlation coefficient analysis. Multiple linear regressions were used to quantify the efficiency of bi-dimensional food web estimates for predicting Hg levels in fish across the study sites. Statistical analyses were performed using Minitab® and SYSTAT® (Wilkinson 2001) software.

RESULTS AND DISCUSSION

Study sites and baseline Hg concentrations

Aqueous Hg concentrations were higher in natural lakes relative to reservoir stations ($t=3.275$, $df=6$, $p=0.017$). Particulate and periphyton [Hg] did not differ between ecosystem types. (Table 4-1).

Table 4-4. Characteristics of the fish communities considered for analysis. Average fork length (FL), age, [Hg], isotope data ($\delta^{13}C$ and $\delta^{15}N$), TrophP and $\%C_{LITT/PEL}$ (means ± SE), with community estimates of Hg concentrations and vertical and horizontal food web structure.

	Natural lakes					Reservoir stations		
	Ashua	**Atik**	**Enaka**	**Mista**	**Papaua**	**Gabbro**	**Lobstick**	**Sandgirt**
n (fish)	48	42	42	42	27	25	35	32
FL (mm)	425 ± 33	414 ± 42	297 ± 24	405 ± 36	438 ± 44	483 ± 41	424 ± 36	437 ± 34
FL-range	67-840	43-900	84-732	65-985	70-930	40-815	27-795	110-840
age (years)	12 ± 1.4	12 ± 1.6	7 ± 0.9	9 ± 1.0	10 ± 1.2	11 ± 1.7	12 ±1.1	12 ± 1.5
age-range	1-38	1-34	1-18	0-27	1-20	1-37	4-32	1-35
Hg (ppm)	0.30 ± 0.04	0.40 ± 0.07	0.13 ± 0.02	0.19 ± 0.03	0.22 ± 0.04	0.38 ± 0.09	0.34 ±0.07	0.34 ± 0.06
Hg-range	0.03-0.91	0.02-1.37	0.02-0.45	0.02-1.15	0.02-0.80	0.03-1.90	0.03-1.80	0.05-1.48
estimates of community Hg	**0.395**	**0.808**	**0.210**	**0.250**	**0.285**	**0.754**	**0.685**	**0.560**
$\delta^{13}C$	-26.6 ± 0.3	-25.5 ± 0.3	-24.6 ± 0.1	-24.8 ± 0.2	-25.2 ± 0.2	-27 ± 0.3	-29.6 ± 0.2	-29.2 ± 0.3
$\delta^{15}N$	8.7 ± 0.3	8.2 ± 0.3	6.1± 0.1	6.4 ± 0.2	7.5 ± 0.3	9.2 ± 0.3	9.7 ± 0.4	10.2 ± 0.3
$\%C_{LITT/PEL}$	27.6 ± 4.5	73.2 ± 3.9	59.4 ± 2.6	33.9 ± 2.0	38.7 ± 2.7	43.1 ±4.4	12.4 ± 2.2	18.1 ± 3.0
$\%C_{LITT/PEL}$-range	0-100	0-100	12-90	9-71	11-70	6-96	0-37	0-59
Estimates of Horizontal food web structure	**36.84**	**100**	**98.96**	**45.18**	**51.19**	**85.59**	**24.91**	**30.17**
TrophP	2.78 ± 0.1	2.82 ± 0.1	2.21 ± 0.03	2.29 ± 0.1	3.10 ± 0.1	2.76 ± 0.1	2.99 ± 0.1	3.05 ± 0.1
TrophP-range	2.1-3.7	2.2-3.7	1.9-3.0	1.5-3.1	2.4-3.8	1.8-3.5	1.8-4.2	2.2-3.8
estimates of Vertical food web structure	**3.70**	**5.65**	**3.69**	**3.06**	**4.11**	**5.48**	**6.25**	**5.08**

Ashua=Ashuapamatikuan Lake, Atik=Atikonak Lake, Enaka=Enakapeshakamau Lake, Mista= Mistashini Lake, Papaua= Papauakamau Lake

Differences in fish Hg concentrations between natural lakes and reservoir stations.

Fish from reservoir stations had higher Hg levels than fish communities in natural lakes (Fig.4-3, Table 4-5). Fish Hg concentrations were comparable among reservoir stations (n=92, $F_{2,89}$=0.079, p=0.92). On a species-specific basis, Hg concentrations were higher in reservoir populations of piscivorous species (Lake Trout and Northern Pike) while benthivores (White and Long Nose Suckers) and a forage fish (White Fish) had comparable Hg levels between ecosystem types (Table 4-5).

Table 4-5. Differences in average Hg concentrations in fish between natural lakes and reservoir stations. Significant differences in means are indicated in bold.

		Natural Lakes		**Reservoir stations**				
	species	n	Mean±SD	n	Mean±SD	t	df	p
Hg (ppm)	all	**201**	**0.249±0.25**	**92**	**0.350±0.38**	**-2.476**	**291**	**0.014**
Hg (ppm)	LNS	51	0.149±0.14	15	0.186±0.15	-0.886	64	0.379
Hg (ppm)	LT	**15**	**0.803±0.31**	**7**	**1.206±0.58**	**-2.149**	**20**	**0.044**
Hg (ppm)	**NP**	**52**	**0.371±0.35**	**27**	**0.563±0.27**	**-2.497**	**77**	**0.015**
Hg (ppm)	WF	26	0.137±0.09	29	0.156±0.11	-0.734	53	0.466
Hg (ppm)	WS	29	0.211±0.16	7	0.117±0.05	1.530	34	0.135

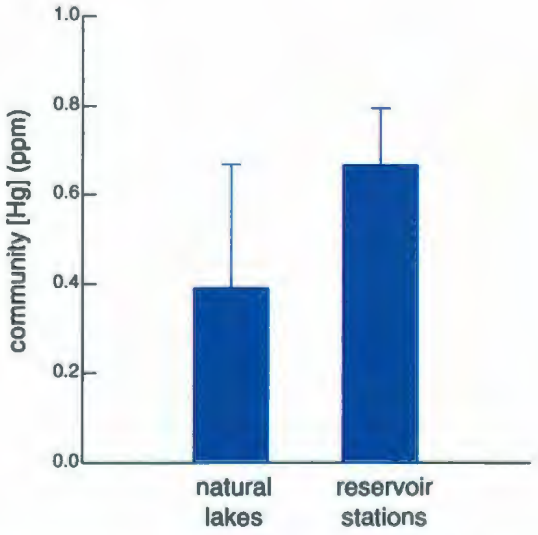

Fig. 4-3. Differences in community estimates of Hg concentrations in fish between natural lakes (n=5) and reservoir stations (n=3). (error bars=std dev).

Average Hg concentrations measured for Lake Trout and Northern Pike in the reservoir exceeded the 0.5ppm limit for safe fish consumption (Table 4-5). The maintenance of high Hg levels in piscivorous Lake Trout and Northern Pike in the CFR was observed 21 years after impoundment by Anderson et al. (1995). Our results indicate that system-specific factors still contribute to maintain higher Hg levels for these species in the CFR reservoir relative to nearby lakes.

Differences in fish Hg concentrations among natural lakes.

Fish Hg levels differed among natural lakes and were higher in fish from Atikonak and lowest in fish from Enakapeshakamau Lake (Fig. 4-4A, Table 4-6). Species-specific differences in Hg concentrations among lakes again were significant in piscivorous Lake Trout and Northern Pike (Table 4-6). Lake Trout were only sampled in two lakes and had Hg body burdens on average greater than 0.5ppm in both lakes (Table 4-6).

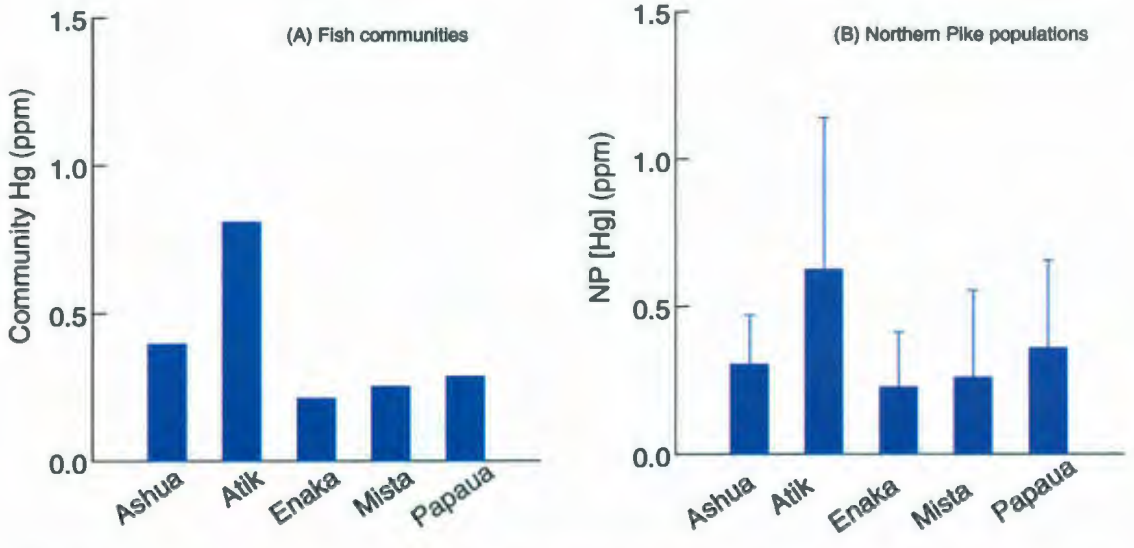

Fig. 4-4. Differences in Hg concentrations in fish among natural lakes. (A) Community estimates of Hg concentrations weighted by species and size class. (B) Average Hg concentrations in Northern Pike populations (error bars=std dev).

Table 4-6. Communities and species-specific differences in average Hg concentrations in fish among natural lakes. Significant differences in means measured as one-way ANOVAS are indicated in bold.

		Ashua		Atik		Enaka		Mista		Papaua				
	species	n	Mean±SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	F-ratio	df*	p-value
Hg (ppm)	**all**	**48**	**0.30±0.25**	**42**	**0.40 ± 0.45**	**42**	**0.13 ± 0.12**	**42**	**0.19 ± 0.22**	**27**	**0.22 ± 0.20**	**6.44**	**4,196**	**<0.001**
Hg (ppm)	BT	0		0		12	0.04 ± 0.02	5	0.05 ± 0.01	3	0.06 ± 0.02	1.59	2,17	0.232
Hg (ppm)	LNS	13	0.20±0.19	8	0.10 ± 0.14	10	0.15 ± 0.10	11	0.14 ± 0.13	9	0.12 ± 0.10	0.83	4,46	0.511
Hg (ppm)	LT	**10**	**0.65±0.18**	**5**	**1.10 ± 0.31**	**0**		**0**		**0**		**13.06**	**1,13**	**0.003**
Hg (ppm)	**NP**	**11**	**0.30±0.16**	**13**	**0.63 ± 0.49**	**5**	**0.23 ± 0.17**	**15**	**0.26 ± 0.29**	**8**	**0.36 ± 0.28**	**2.80**	**4,47**	**0.036**
Hg (ppm)	WF	14	0.12 ± 0.07	12	0.16 ± 0.11	0		0		0		1.42	1,24	0.245
Hg (ppm)	WS	0		1	0.33	10	0.19 ± 0.14	11	0.21 ± 0.20	7	0.24 ± 0.15	0.32	3,25	0.808

See Table 4-1 for lake and species legend. df*=numerator, denominator degrees of freedom.

Table 4-7. Differences in the carbon isotopic compositions ($\delta^{13}C$) of primary producers and primary consumers among natural lakes. $\delta^{13}C_{littoral}$ and $\delta^{13}C_{pelagic}$ indicate organisms used as littoral and pelagic isotopic endpoints, respectively. Significant differences in means are indicated in bold.

	Ashua		Atik		Enaka		Mista		Papaua				
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	F-ratio	df	p-value
Periphyton ($\delta^{13}C_{littoral}$)	4	-23.43 ± 0.14	4	-23.93 ± 0.39	4	-22.35 ± 0.71	4	-18.75 ± 0.51	4	-19.63 ± 0.39	24.48	4,15	**<0.001**
SPM+53µm ($\delta^{13}C_{pelagic}$)	4	-27.33 ± 0.89	4	-30.11 ± 0.33	3	-27.81 ± 0.61	4	-27.93 ± 0.45	4	-28.73 ± 0.32	3.93	4,14	**0.024**
SPM	2	-25.80 ± 0.20	2	-30.20 ± 0.80	2	-28.43 ± 0.08	2	-28.65 ± 0.30	2	-28.35 ± 0.40	13.36	4,5	**0.007**
53µm	2	-28.85 ± 0.15	2	-30.02 ± 0.07	1	-26.60	2	-27.15 ± 0.24	2	-29.10 ± 0.40	26.18	4,4	**0.004**
100µm	2	-30.01 ± 1.12	2	-32.10 ± 0.34	1	-27.30	2	-26.64 ± 0.54	2	-29.13 ± 0.27	10.17	4,4	**0.023**
200µm	2	-31.33 ± 0.56	2	-31.90 ± 0.05	1	-29.45	2	-28.13 ± 0.23	2	-28.67 ± 0.34	22.46	4,4	**0.005**
500µm	2	-31.26 ± 0.11	2	-31.81 ± 0.45	1	-30.07	2	-29.51 ± 0.33	2	-29.23 ± 0.03	15.31	4,4	**0.011**

df*=numerator, denominator degrees of freedom

Northern Pike were found in all lakes and average Pike Hg levels only exceeded the 0.5ppm advisory limit in Atikonak Lake (Table 4-6). Among-lake variations in average Hg concentrations in Northern Pike were similar to community-scale variations (Fig. 4-4). This is because Northern Pike is a Quis-type consumer whose ontogeny determines relatively constant spatially-explicit (bi-dimensional) dietary pathways of Hg intake among ecosystems (Chapter 3). Patterns of Hg accumulation in Northern Pike thereby reflect differences in Hg availability and exposure among lakes, making the species a good indicator of inter-system effects on Hg bioaccumulation.

Autochthonous-allochthonous carbon source contributions at the base of food webs influence Hg levels in fish.

The carbon isotopic compositions of primary producer/consumer were depleted in reservoir stations relative to natural lakes (Fig. 4-5, Table 4-8).

Table 4-8. Differences in the carbon isotopic compositions ($\delta^{13}C$) of primary producers and primary consumers (periphyton, particulate, and plankton size-fractions) between natural lakes and reservoir stations. $\delta^{13}C_{littoral}$ and $\delta^{13}C_{pelagic}$ indicate organisms used as littoral and pelagic isotopic endpoints, respectively. Significant differences in means are indicated in bold.

	Natural lakes		**Reservoir stations**				
	n	Mean ± SE	n	Mean ± SE	t	df	p-value
Periphyton ($\delta^{13}C_{littoral}$)	20	**-21.62** ± 0.51	9	**-24.39** ± 0.35	3.473	27	**0.002**
SPM+53µm ($\delta^{13}C_{pelagic}$)	19	**-28.41** ± 0.32	6	**-29.72** ± 0.17	2.232	23	**0.036**
SPM	10	-28.29 ± 0.49	3	-29.43 ± 0.17	1.232	11	0.243
53µm	9	-28.54 ± 0.43	3	-30.02 ± 0.19	1.908	10	0.086
100µm	9	-29.22 ± 0.73	3	-31.70 ± 0.22	1.891	10	0.088
200µm	9	**-29.94** ± 0.56	3	**-32.18** ± 0.14	2.233	10	**0.050**
500µm	9	**-30.41** ± 0.38	3	**-32.15** ± 0.25	2.507	10	**0.031**

Differences in $\delta^{13}C$ between ecosystem types were statistically significant in littoral periphyton, in pelagic isotopic baselines (SPM+53µm-plankton) and in ≥200µm and ≥500µm plankton fractions (Table 4-8). These numbers indicate greater contributions of ^{13}C-depleted autochthonous carbon of algal or microbial origin in reservoir food webs relative to natural lakes.

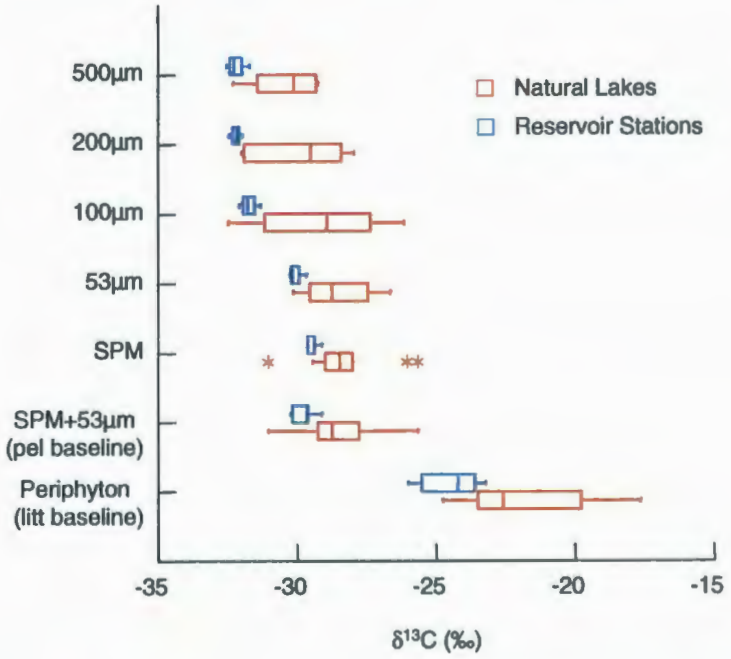

Fig. 4-5. Differences in the carbon isotopic compositions of primary producers and primary consumers between natural lakes and reservoir stations.

In reservoir systems, bacterial growth and activity is stimulated by the release of labile carbon and nutrients from flooded soils and vegetation (Jackson 1991, Tremblay and Lucotte 1997). Annual draw-downs causing periodic mixing further support the abundance and availability of ^{13}C-depleted respired CO_2 for uptake by primary producers. Transient peaks of elevated algal productivity (as linked to pulses of inorganic nutrient release caused by the resuspension of epilimnetic sediments during reflooding (Turner et

al. 2005)), may also sustain higher rates of microbial respiration in reservoir food webs relative to natural lakes. Thus while allochthonous carbon typically dominate aquatic food web production in boreal environments (France 1997, Wetzel 2001, Carpenter et al. 2005), our results signify the importance of autochthonous microbial pathways for carbon uptake in reservoir ecosystems. In the Labrador CFR reservoir, we suggest that abundant organic matter caused by the initial flooding of entire spruce forests, together with annual draw-down cycles and potential pulses of enhanced algal productivity, continue to support important microbial activity and carbon pathways to lower trophic levels.

Compositional (autochthonous-allochthonous) differences in available carbon at the food web base may be linked to differences in Hg bioavailability among ecosystems. Montgomery et al. (2000) observed higher levels of autochthonous carbon in the fine particulate matter and zooplankton of boreal reservoirs relative to natural lakes. Zooplankton and particulate $\delta^{13}C$ then varied negatively with their methylmercury (MeHg) concentrations, indicating greater Hg availability in reservoir systems characterized by higher levels and assimilation of ^{13}C-depleted carbon of autochthonous origin (Montgomery and al. 2000). In our study sites, fish Hg concentrations were similarly negatively related to pelagic (SPM+53μm-plankton) and littoral (periphyton) isotopic endpoints $\delta^{13}C$ signatures (Fig. 4-6A and 4-6B). This indicated greater Hg bioaccumulation in fish from reservoir sites with greater contributions of autochthonous-recycled (as opposed to bulk-allochthonous) carbon at the base of food webs. Similar trends were observed among natural lakes (Fig. 4-6C and 4-6D). Primary producer/consumer carbon isotopic signatures also differed among lakes (Table 4-7).

Lighter $\delta^{13}C$ values indicating greater assimilation of ^{13}C-depleted autochthonous carbon characterized the lower food webs of Atikonak and Ashuapamatikuan lakes, where fish also reached higher Hg concentrations.

(A) $$\mathbf{Log[Hg]_{fish} = -3.37-0.0893(\delta^{13}C_{SPM+53\mu m\text{-}plankton})}$$
(n=293, F=12.105, p=0.001, r^2=0.040)

(B) $$\mathbf{Log[Hg]_{fish} = -1.90-0.0485(\delta^{13}C_{periphyton})}$$
(n=293, F=15.202, p=0.000, r^2=0.050)

(C) $$\mathbf{Log[Hg]_{fish} = -2.74-0.0665(\delta^{13}C_{SPM+53\mu m\text{-}plankton})}$$
(n=201, F=3.973, p=0.048, r^2=0.020)

(D) $$\mathbf{Log[Hg]_{fish} = -1.85-0.0456(\delta^{13}C_{periphyton})}$$
(n=201, F=7.909, p=0.005, r^2=0.038)

Fig. 4-6. Linear relationships between fish Hg concentrations and the carbon isotopic compositions of littoral and pelagic primary producers ($\delta^{13}C_{periphyton}$ and $\delta^{13}C_{SPM+53\mu m\text{-}plankton}$) in the study sites. (A) and (B): lakes and reservoir stations combined (C) and (D): among natural lakes only.

Linear relationships between fish Hg and primary producers' $\delta^{13}C$ however had low predictive (r^2) values (Fig. 4-6). This signifies the influence of carbon source on Hg in fish is complex. The magnitude of allochthonous subsidies to aquatic food webs is determined by physical ecosystem structure (Polis et al. 1997, Schindler and Scheuerell 2002), by spatially-explicit resource utilization in primary consumers (Matthews and Mazumder 2006), by inter-system differences in bacterial growth and biomass transfer to higher trophic levels (Karlsson 2007) and by the edible character of allochthonous carbon source (Pace et al. 2004). For Hg pathways to aquatic biota, the key link is through

bacterial activity that stimulates methylation processes affecting Hg bioavailability (Ullrich et al. 2001). Greater assimilation of ^{13}C-depleted respired CO_2 by primary producers may be an indication of enhanced bacterial growth and Hg methylation, as well as of greater microbial biomass and MeHg transfers to primary consumers leading to greater Hg contamination. Carbon source dynamics as carbon subsidies from surrounding landscapes, algal productivity and within-system carbon recycling, thus affect Hg bioavailability at the base of aquatic food webs and the extent of Hg bioaccumulation in fish. We suggest that inter-system variations in the importance of carbon recycling, bacterial biomass and Hg transfers to aquatic biota, may explain differences in Hg exposure and accumulation in fish among natural lakes, and the maintenance of elevated Hg levels in fish in reservoir ecosystems.

Can bi-dimensional food web structure explain inter-system differences in the extent of Hg bioaccumulation in fish communities?

Autochthonous-allochthonous carbon source dynamics influence Hg availability and assimilation at the base of aquatic food webs. At the level of fish consumers, Hg exposure, uptake and trophic transfers are moreover influenced by species-specific biological features and bi-dimensional (spatially-explicit) feeding strategies (Chapter 3).

Biological features

The mean age and fork length of fish communities were comparable among reservoir stations (for FL: $F_{2,89}$=0.66, p=0.52; for Age: $F_{2,78}$=0.32, p=0.73) and between natural lakes and reservoir stations (for FL: t=-1.837, df=291, p=0.067; for Age: t=-1.820, df=255, p=0.070). Among natural lakes only, fish from Enakapeshakamau Lake were

significantly smaller and younger relative to other lakes (for FL: $F_{4,196}$=2.53, p=0.042; for Age: $F_{4,171}$=2.84, p=0.026) and had lower Hg concentrations. In Northern Pike and Lake Trout, average fork lengths were similar between ecosystem types and among natural lakes ((between ecosystem types) NP FL: t=-0.564, df=77, p=0.58; LT FL: t=0.693, df=20, p=0.50; (among lakes) NP FL: $F_{4,47}$=0.90, p=0.47; LT FL: $F_{1,13}$=1.81, p=0.20). The mean age of Northern Pike was also comparable among lakes (NP Age: $F_{4,44}$=0.59, p=0.67) and between lakes and the reservoir (NP Age: t=-1.738, df=73, p=0.09). The mean age of Lake Trout was similar among lakes (LT age: $F_{1,12}$=0.08, p=0.78) but differed between lakes and reservoir stations (LT Age: t=2.370, df=19, p=0.029). Lake Trout were comparatively younger (mean age=12+) in the reservoir relative to natural lakes (mean age=19+), whilst having greater Hg body burdens. Patterns of Hg accumulation with fish fork length were similar between lakes and reservoir stations (GLM (Log_{10}Hg*(fish FL*system_type)): n=293, $F_{1,289}$=0.67, p=0.41) and among lakes only (GLM (Log_{10}Hg*(fish FL*lake)): n=201, $F_{4,191}$=1.11, p=0.35) (Fig. 4-7). Patterns of Hg accumulation with fish age differed between ecosystem types (GLM (Log_{10}Hg*(fish age*system_type)): n=257, $F_{1,253}$=16.36, p<0.001) and among natural lakes (GLM (Log_{10}Hg*(fish age*lake)): n=176, $F_{4,166}$=7.19, p<0.001). Lower slopes values of Hg-age relationships characterized fish in the CFR reservoir relative to natural lakes, as well as fish in Atikonak and Ashuapamatikuan relative to other lakes (Fig. 4-7). These patterns demonstrate greater Hg exposure and accumulation in fish from younger age groups in ecosystems reaching higher Hg contamination. Considerations of fish biological features thus signify that system-specific factors were linked to differences in Hg exposure for fish across the study sites.

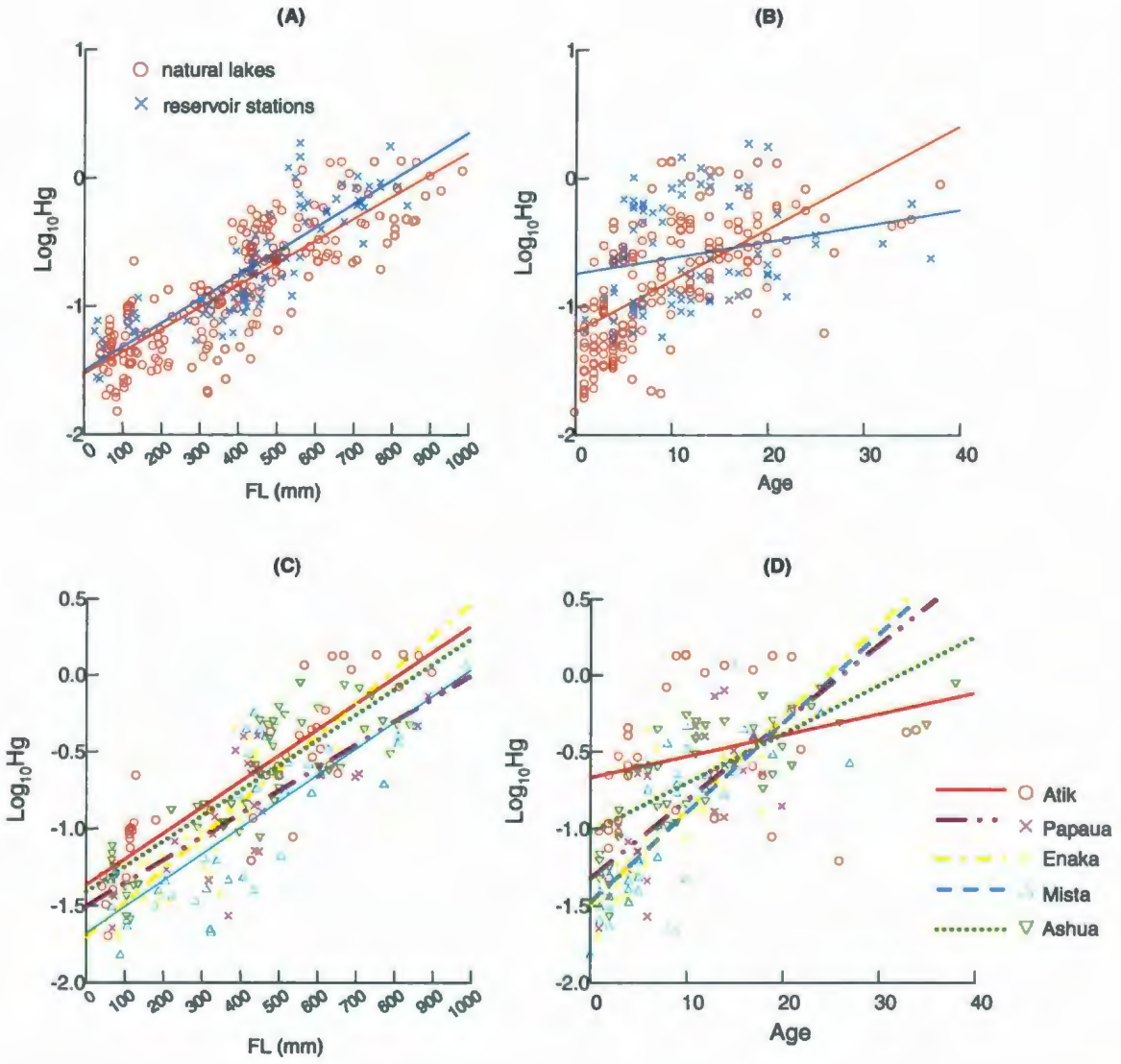

Fig. 4-7. Patterns of Hg accumulation in fish with fork length and age. (A) Hg-FL between reservoir and lakes (lakes: $Log_{10}Hg=-1.54 + 0.00173(FL)$ ($F_{1,199}=433.87$, $p<0.001$, $r^2=0.68$); reservoir: $Log_{10}Hg=-1.50 + 0.00186(FL)$ ($F_{1,90}=241.51$, $p<0.001$, $r^2=0.73$)). (B) Hg-age between reservoir and lakes (lakes: $Log_{10}Hg=-1.21 + 0.0404(age)$ ($F_{1,174}=119.42$, $p<0.001$, $r^2=0.40$); reservoir: $Log_{10}Hg=- 0.746 + 0.0126(age)$ ($F_{1,79}=4.34$, $p=0.04$ $r^2=0.04$)). (C) Hg-FL among lakes (Ashua: $Log_{10}Hg=-1.41 + 0.00164(FL)$ ($F_{1,46}=126.00$, $p<0.001$, $r^2=0.73$); Atik: $Log_{10}Hg=-1.37 + 0.00168(FL)$ ($F_{1,40}=140.53$, $p<0.001$, $r^2=0.77$); Enaka: $Log_{10}Hg=-1.71 + 0.00217(FL)$ ($F_{1,40}=123.91$, $p<0.001$, $r^2=0.75$); Mista: $Log_{10}Hg=-1.68 + 0.00171(FL)$ ($F_{1,40}=69.67$, $p<0.001$, $r^2=0.63$); Papaua: $Log_{10}Hg=-1.51 + 0.00150(FL)$ ($F_{1,25}=43.62$, $p<0.001$, $r^2=0.62$)). (D) Hg-age among lakes (Ashua: $Log_{10}Hg=-1.02 + 0.0319(age)$ ($F_{1,38}=44.89$, $p<0.001$, $r^2=0.53$); Atik: $Log_{10}Hg =-0.668 + 0.0138(age)$ ($F_{1,31}=2.69$, $p=0.11$, $r^2=0.05$); Enaka: $Log_{10}Hg=-1.50 + 0.0605(age)$ ($F_{1,35}=65.51$, $p<0.001$, $r^2=0.64$); Mista: $Log_{10}Hg=-1.48 + 0.0582(age)$ ($F_{1,39}=52.26$, $p<0.001$, $r^2=0.56$); Papaua: $Log_{10}Hg=-1.33 + 0.0507(age)$ ($F_{1,23}=20.27$, $p<0.001$, $r^2=0.45$)).

Bi-dimensional food web structures

On average, reliance on littoral versus pelagic carbon by fish communities differed among natural lakes, reservoir stations, and between lakes and the reservoir (Table 4-9). Mean trophic positions of fish were similar among reservoir stations but differed among lakes and between lakes and the reservoir (Table 4-9).

Table 4-9. Differences in mean trophic position (TrophP) and littoral-pelagic resource use ($\%C_{LITT/PEL}$) among fish communities. (A) lakes and reservoir stations, (B) natural lakes (C) reservoir stations. Significant differences in mean are indicated in bold.

(A)

	Natural Lakes			Reservoir stations					
	n	Mean ± SD	Range	n	Mean ± SD	Range	t	df	p
$\%C_{LITT/PEL}$	201	**46.6** ± 1.98	(0-100)	92	**22.7** ± 2.22	(0-95.7)	7.239	291	**<0.001**
TrophP	201	**2.6** ± 0.04	(1.5-3.8)	92	**2.9** ± 0.06	(1.8-4.2)	-4.971	291	**<0.001**

(B)

	Ashua		Atik		Enaka		Mista		Papaua				
	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	F	p
$\%C_{LITT/PEL}$	48	27±4.5	42	73±3.9	42	59±2.6	42	34±2.0	27	39±2.7	201	31.95	**<0.001**
TrophP	48	2.8±0.1	42	2.8±0.1	42	2.2±0.03	42	2.3±0.1	27	3.1±0.1	201	28.12	**<0.001**

(C)

	Gabbro		Lobstick		Sangirt				
	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	F	p
$\%C_{LITT/PEL}$	25	**43** ± 22	35	**12** ± 13	32	**18** ± 17	92	25.06	**<0.001**
TrophP	25	2.76 ± 0.47	35	2.99 ± 0.66	32	3.05 ± 0.45	92	2.12	0.126

Bi-dimensional food web structure corresponds to the sum of individual fish species trophic position (vertical resource use) and reliance on littoral-pelagic carbon source (horizontal resource use) weighted by size class and sample sizes (see Chapter 2). Site-specific bi-dimensional food web structures are shown in Fig. 4-8.

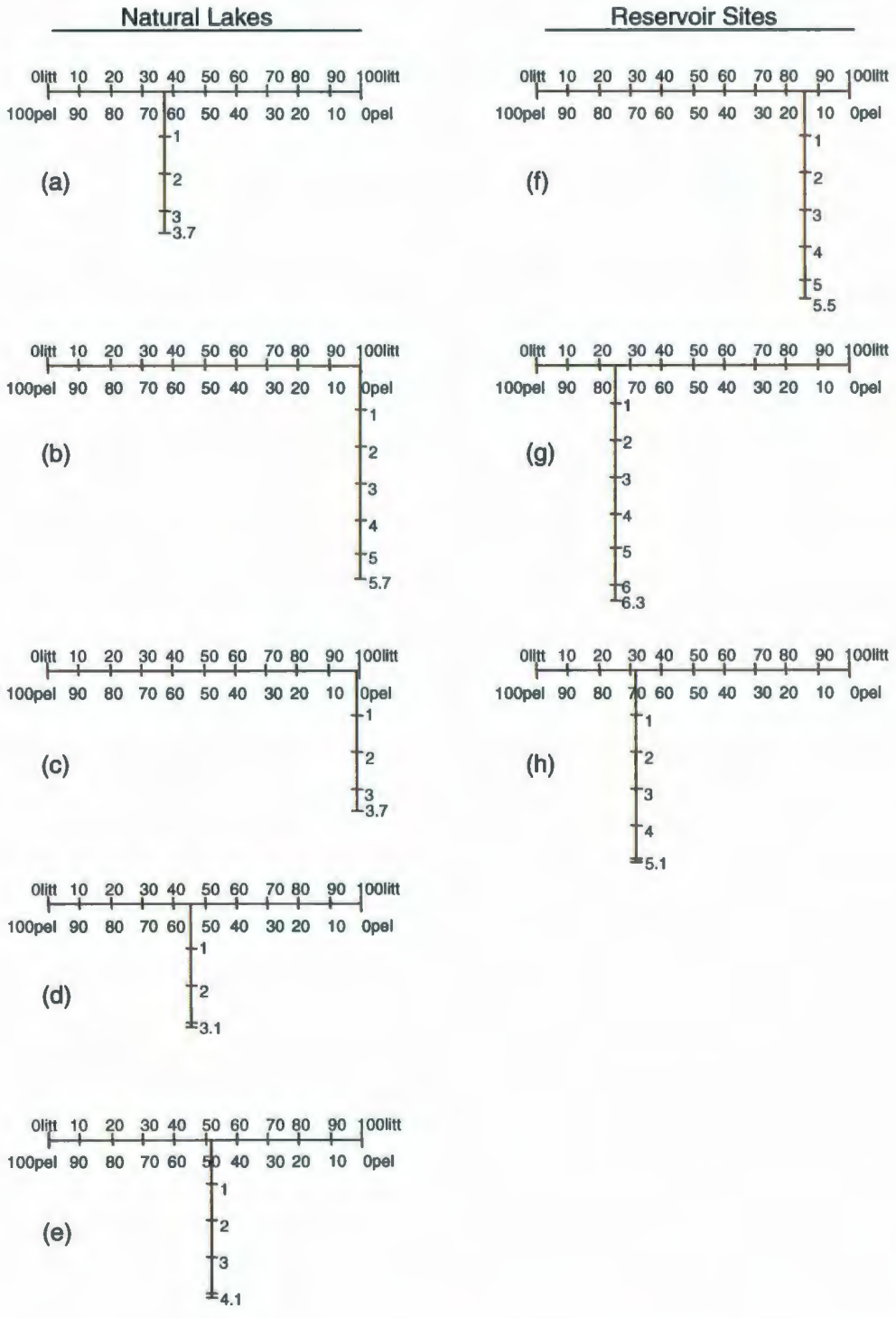

Fig. 4.8. Site-specific bi-dimensional food web structures. (a-e) natural lakes: (a) Ashuapamatikuan, (b) Atikonak, (c) Enakapeshakamau, (d) Mistashini, and (e) Papauakamau. (f-h) CFR reservoir stations: (f) Gabbro, (g) Lobstick and (h) Sandgirt.

Estimates of vertical food web structure were greater in reservoir stations (Table 4-4). This indicated longer food chains in the reservoir relative to natural lakes. Based on ecosystem size and productivity hypothesis (Vander Zanden et al. 1999, Post et al. 2000b), longer food chains in the reservoir may be linked to its very large surface area and abundance of nutrients (as leached from flooded soils (Turner et al. 2005), provided by the decomposition of drowned vegetation (Baxter 1977), and/or linked to greater nutrient influx from larger drainage basins (Wetzel 2001)). A difference in vertical food web structure corresponding to longer food chains may explain greater Hg biomagnification in reservoir fish relative to nearby lakes (Cabana et al. 1994, Cabana and Rasmussen 1994). Patterns of Hg accumulation with fish trophic position however, were nearly identical between ecosystem types (Fig. 4-9A). In contrast, patterns of Hg accumulation with fish reliance on littoral-pelagic carbon source differed between natural lakes and reservoir stations (GLM ($Log_{10}Hg$*(%$C_{LITT/PEL}$*system_type)): n=293, $F_{1,289}$=13.39, $p<0.001$) (Fig. 4-9B). Hg concentrations in reservoir fish increased with littoral resource use. This relationship was significant and similar among reservoir stations, explaining between 30% and 42% of the variability in fish Hg levels (Fig. 4-9C). Greater Hg contamination was observed in fish from Gabbro station in the older (Ossokmanuan) portion of the CFR reservoir, where vertical energy flows were sustained by dominant-littoral (as opposed to dominant-pelagic) carbon source (Fig. 4-8). These results indicate greater Hg exposure via littoral dietary pathways for fish in the reservoir ecosystem, and enhanced Hg bioaccumulation in reservoir food webs deriving most of their carbon from the littoral habitat.

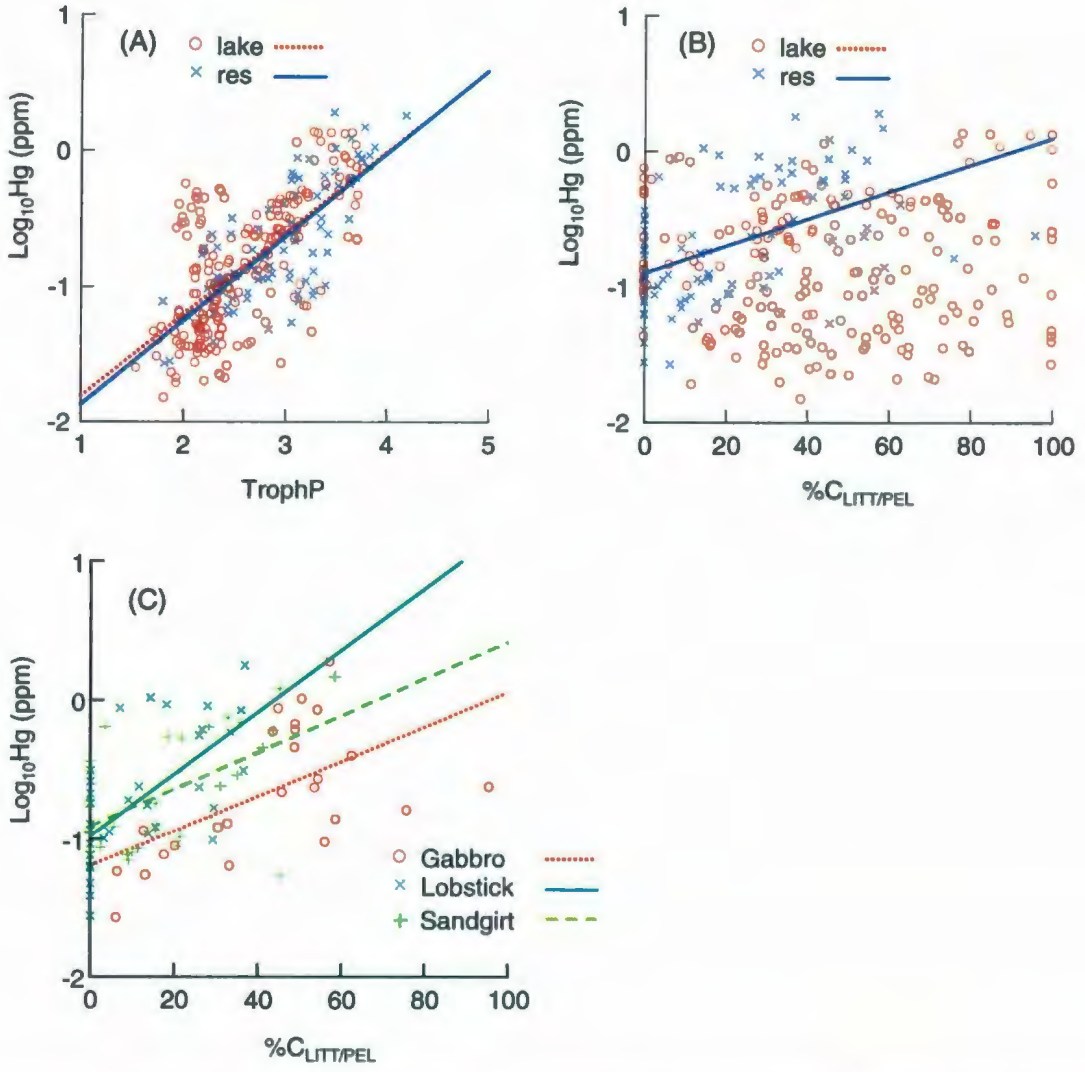

Fig. 4-9. Patterns of Hg accumulation in fish with trophic position (TrophP) and reliance on littoral-pelagic carbon source ($\%C_{LITT/PEL}$). (A) Hg-TrophP between lakes and reservoir stations (lakes: $Log_{10}Hg=-2.42 + 0.599(TrophP)$ (n=201, F=157.34, p<0.001, $r^2=0.44$); reservoir: $Log_{10}Hg=-2.49 + 0.614(TrophP)$ (n=92, F=127.21, p<0.001, $r^2=0.59$)). (B) Hg-$\%C_{LITT/PEL}$ between lakes and reservoir stations (lakes: no relationship; reservoir: $Log_{10}Hg=-0.905 + 0.00997(\%C_{LITT/PEL})$ (n=92, F=27.22, p<0.001, $r^2=0.23$)). (C) Hg-$\%C_{LITT/PEL}$ among reservoir stations (Gabbro: $Log_{10}Hg=-1.20 + 0.0125(\%C_{LITT/PEL})$ (n=25, F=11.34, p=0.003, $r^2=0.33$); Lobstick: $Log_{10}Hg=-0.977 + 0.0222(\%C_{LITT/PEL})$ (n=35, F=24.09, p<0.001, $r^2=0.42$), Sandgirt: $Log_{10}Hg=-0.907 + 0.0133(\%C_{LITT/PEL})$ (n=32, F=13.13, p=0.001 $r^2=0.30$)).

Greater Hg exposure via littoral dietary pathways may be linked to primary productivity limitations and/or to the importance of heterotrophic processes in littoral periphyton. Littoral-benthic primary productivity is limited in hydroelectric reservoirs (Baxter 1977,

Black et al. 2003, Turner et al. 2005). This is due to detrimental impacts of water level fluctuations on littoral-benthic primary producers, which can cause periodic desiccation, habitat disruption, loss of colonizing substrate and transient periods of light limitation (as per increased abiogenic turbidity) during re-flooding (Baxter 1977, Wetzel 2001, Black et al. 2003, Turner et al. 2005). Lower primary productivity is linked to lower Hg biodilution and so greater Hg availability in littoral periphyton (Desrosiers et al. 2006a). At the time of sampling, periphyton biomass in reservoir stations did not differ from natural lakes but were negatively related to periphyton Hg (in all sites: n=8, r=-0.480, p=0.288; among reservoir stations: n=3, r=-0.973, p=0.150). The lack of statistical significance of these correlations is likely due to our small sample number. Alternatively, important auto-heterotrophic coupling in reservoir periphyton (as indicated by comparatively depleted periphyton $\delta^{13}C$ values) may favor Hg methylation and transfers to primary consumers and fish via littoral dietary pathways. Seasonal differences in draw-down cycles between Gabbro station (in Ossokmanuan) and Lobstick and Sandgirt stations (in the Smallwood reservoir) are probably responsible for the greater periphyton biomass and reliance on littoral carbon by Gabbro fish at the time of sampling (mid-summer), when Gabbro station was being emptied and Lobstick and Sandgirt stations were being filled.

Together, fish fork length, vertical trophic position and horizontal reliance on littoral-pelagic carbon source explained 80% of the variations in fish Hg concentrations in the reservoir ecosystem (Fig. 4-10A). The same variables, together with fish age, explained 75% of the variability in fish Hg levels across all study sites (Fig. 4-10B). To our

knowledge, this is a good approximation of inter-system variations in fish Hg concentrations without distinction of species, ecosystem type, and physical and chemical ecosystem structure. Yet among natural lakes only, horizontal littoral-pelagic resource use by fish was not linearly related to inter-system differences in fish Hg contamination. Horizontal reliance on littoral-pelagic carbon source had a significant influence on lake fish Hg levels only when considered a lake-specific feature (GLM for LogHg*(%$C_{LITT/PEL}$*Lake): n=201, $F_{4,191}$=4.20, p=0.003). Bi-dimensional food web structures were highly variable among lakes. Vertical energy flows were sustained by dominant-pelagic carbon source in one lake (Ashuapamatikuan), by almost equivalent littoral-pelagic contributions in two lakes (Mistashini and Papaukamau) and by dominant-littoral carbon source in two other lakes (Atikonak and Enakapeshakamau). In Chapter 2, we have shown that such differences in bi-dimensional food web structures among ecosystems are linked to spatial patterns in physical ecosystem characteristics and consumer community composition. In the study lakes, estimates of horizontal food web structure were highly correlated to lake perimeter to area ratio (n=5, r=0.982, p=0.003), indicating greater reliance on littoral carbon in lakes characterized by important littoral habitat dimensionality. Using a distinction of community composition and lake PAratio together with fish fork length and age in a linear model, explained a similar amount of variability (74%) in fish Hg levels as stable-isotope estimates of fish trophic position and percent reliance on littoral-pelagic carbon source across the study sites (Fig. 4-10C). It also explained 78% of the variability in fish Hg concentrations among natural lakes only (Fig. 4-10D). These models predict greater Hg concentrations in larger and older fish in ecosystems with more elaborate fish communities (and thus longer food chains) and

greater littoral habitat dimensionality (and thus greater reliance on littoral carbon). This is an important finding, as the evaluation of physical habitat structure and fish community composition among ecosystems or biogeographic regions, is relatively straightforward and inexpensive.

For the reservoir ecosystem:

(A) $\mathbf{Log_{10}Hg = -2.11 + 0.00122(FL) + 0.00246(\%C_{LITT/PEL}) + 0.282(TrophP)}$

(n=92, F=119.86, p<0.001, r^2_{adj}=**0.797**)

(FL: t=7.99, p<0.001, $\%C_{LITT/PEL}$: t=2.22, p=0.029, TrophP: t=5.45, p<0.001)

For all sites (natural lakes and reservoir stations):

(B) $\mathbf{Log_{10}Hg = -2.12 + 0.00118(FL) + 0.0151(Age) + 0.00113(\%C_{LITT/PEL}) + 0.234(TrophP)}$

(n=257, F=189.26, p<0.001, r^2_{adj}=**0.746**)

(FL: t=11.05, p<0.001, Age: t=6.87, p<0.001, $\%C_{LITT/PEL}$: t=2.16, p=0.03, TrophP: t=6.46, p<0.001)

For all sites (natural lakes and reservoir stations):

(C) $\mathbf{Log_{10}Hg = -1.78 + 0.00156(FL) + 0.0119(Age) + 0.175(Com\_type) + 0.0593(PAratio)}$

(n=257, F=181.47, p<0.001, r^2_{adj}=**0.738**)

(FL: t=19.01, p<0.001, Age: t=5.32, p<0.001, Com_type: t=5.54, p<0.001, Paratio: t=1.94, p=0.05)

For natural lakes:

(D) $\mathbf{Log_{10}Hg = -1.78 + 0.00138(FL) + 0.0183(Age) + 0.178(Com\_type) + 0.0657(PAratio)}$

(n=176, F=151.38, p<0.001, r^2_{adj}=**0.775**)

(FL: t=15.25, p<0.001, Age: t=6.97, p<0.001, Com_type: t=4.86, p<0.001, Paratio: t=2.03, p=0.04)

Fig. 4-10. Models for predicting fish Hg concentrations in boreal aquatic ecosystems, using fish biological features (FL and Age), vertical trophic position (TrophP) and horizontal reliance on littoral versus pelagic carbon sources ($\%C_{LITT/PEL}$). (A) Linear model using fish fork length (FL), TrophP and $\%C_{LITT/PEL}$ to predict Hg concentrations in fish in the CFR reservoir ecosystem. (B) Linear model using fish FL, age, TrophP and $\%C_{LITT/PEL}$ to predict Hg concentrations in fish across all study sites (natural lakes and reservoir stations combined). (C)-(D) Linear models using fish FL, age, a binary measure of community composition (Com_type) and perimeter to area ratio (PAratio) to predict Hg concentrations in fish (C) across all study sites and (D) among natural lakes.

The small amount of variability in fish Hg that was explained by littoral-pelagic resource use or PAratio in community-scale models is due to species-specific differences in cross-habitat feeding patterns and Hg uptake. Spatially-explicit dietary pathways of Hg accumulation in fish are complicated by among-species variations in the type and size of prey consumed between habitat boundaries (Chapter 3). Yet in spite of inherent species-specific and inter-system complexities, bi-dimensional food web structures (or ecosystem features affecting the extent of vertical energy flows and cross-habitat foraging by fish) increased the predictive capacities of linear models explaining inter-system variations in fish Hg concentrations. In all cases, littoral resource use (and larger PAratios promoting littoral resource use) were linked to greater Hg contamination in fish. Even among lakes, average Hg concentrations in Northern Pike only exceeded the 0.5ppm limit for safe fish consumption in the one lake (Atikonak) where vertical trophic organization was entirely supported by littoral carbon source (Fig. 4-8b). These findings demonstrate that littoral dietary pathways support greater Hg bioaccumulation in fish in boreal aquatic ecosystems.

Further implications

Bi-dimensional food web structures estimated from vertical and horizontal resource use in fish communities (or from ecosystem-specific features determining trophic positions and cross-habitat foraging by fish), can improve the evaluation of spatial variations in fish Hg contamination. On a temporal scale not considered in this study, we suggest that changes in bi-dimensional food web structures may further serve to explain inter-system

differences in the extent of Hg bioaccumulation. Changes in bi-dimensional food web structure provide alternative stable states that serve to maintain populations and community integrity in spite of changing ecosystem conditions (Chapter 2). Flexibility in bi-dimensional food web structure is determined by the sum of consumer species bi-dimensional feeding strategies classified by autecological types (Chapter 2). In the CFR reservoir, the sum of represented fish species autecological types corresponds to Aequivocus-dominant communities (Fig. 4-11). This community type should be characterized by intermediate flexibility in bi-dimensional food web structure, depending on physical ecosystem characteristics and community interactions (see Chapter 1 and Chapter 2). The significance of littoral carbon-Hg fluxes to reservoir fish may be enhanced by some adaptation-response of reservoir communities to the intermittent pulse of increased resource availability that characterizes littoral habitats in reservoir systems (Yang et al. 2008). Transient changes in bi-dimensional food web structures permitting greater reliance on littoral carbon source when these are available, could maximize littoral pathways of Hg intake for fish in the CFR reservoir, whilst contributing to maintain the integrity of reservoir fish communities.

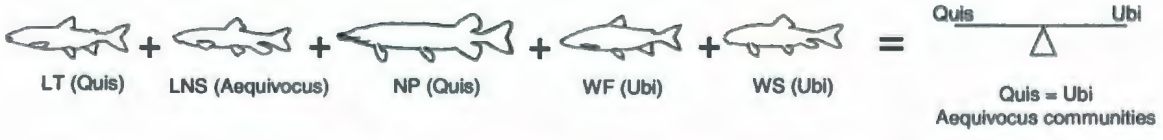

Fig. 4-11. Cumulative autecological types for represented fish species in CFR reservoir communities. Autecological types distinguish consumer bi-dimensional feeding strategies as determined mainly by ontogeny (Quis type), by ecosystem features (Ubi type) or both (Aequivocus type) (Chapter 1). At the food web level, cumulative autecological types determine flexibility in bi-dimensional food web structure (Chapter 2). CFR reservoir fish communities are characterized by a balance between Quis and Ubi type consumers, corresponding to Aequivocus-type communities where bi-dimensional food web structures are equally determined by species and ecosystem characteristics.

In this context, the greater littoral habitat dimensionality of Gabbro station (as indicated by its larger PAratio) would not only permit greater littoral resource exploitation by fish, but facilitate transient changes in bi-dimensional food web structure by limiting the intensity of community interactions in the littoral habitat. Community interactions were shown to affect bi-dimensional resource utilization in Aequivocus-type consumers (Chapter 1), and may similarly affect changes in bi-dimensional food web structure in Aequivocus-type communities.

This study has shown that lower Hg biodilution and/or important microbial processes enhanced Hg availability, exposure and trophic transfers to fish via littoral dietary pathways in the CFR reservoir. We suggest that transient changes in bi-dimensional food web structure may further intensify this Hg accumulation pathway in reservoir food webs, while assisting in maintaining fish populations in such cyclically perturbed ecosystems. Further work in this direction should focus on characterizing temporal variations in bi-dimensional food web structure, and assess how this relates to community stability and patterns of Hg accumulation.

CONCLUSION

Hg concentrations in piscivorous Lake Trout and Northern Pike continue to exceed the advisory limit of 0.5ppm for safe consumption in the Churchill Falls Reservoir and in certain lake ecosystems of Labrador. Our results demonstrate that the maintenance of elevated Hg levels in fish in the reservoir ecosystem, even 33 to 43 years after

impoundment, is related to (i) greater contributions of autochthonous-respired carbon to reservoir food webs and potential respired carbon-MeHg coupling in lower trophic levels; (ii) greater Hg exposure for younger fish in the reservoir; (iii) longer food chains amplifying Hg biomagnification, and (iv) greater Hg availability and exposure via littoral dietary pathways in the reservoir, that may be further enhanced by important reliance on littoral carbon and Hg sources by reservoir fish when these are available. In natural lakes, greater incorporation of autochthonous carbon by primary producers also positively affected the extent of Hg bioaccumulation in fish. Differences in fish Hg concentrations among lakes however were not linearly related to horizontal littoral-pelagic resource use in fish communities. This is due to inter-system differences in Hg bioavailability at the base of littoral and pelagic habitats in lakes, and to inter-specific differences in the type and size of prey consumed across habitat boundaries. Still, our analysis permitted to demonstrate that using ecosystem features affecting vertical and horizontal resource exploitation in fish communities (i.e. community composition and a measure of physical ecosystem structure such as lake perimeter to area ratio) together with fish biological traits (FL and age), can facilitate and improve predictions of fish Hg levels among boreal aquatic ecosystems. Littoral resource use was a positive predictor of fish Hg concentrations in the study sites, and was enhanced by littoral habitat dimensionality. This underlined the importance of littoral periphyton, littoral dietary pathways and littoral habitat structure, for determining Hg bioaccumulation in fish in boreal aquatic environments.

Our study demonstrates the utility of distinguishing carbon sources and the application of a bi-dimensional approach to food web structure for facilitating the evaluation of spatial

variations in Hg bioaccumulation among fish communities used for subsistence fishing. Further work is now required to evaluate temporal changes in bi-dimensional food web structure and to assess how this relates to community resilience and contaminants bioaccumulation. Based on the evidence presented in this chapter, we believe our bi-dimensional approach can serve as a conceptual basis to elaborate larger-scale models for managing Hg contamination and human exposure across landscapes.

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THESIS SUMMARY

This thesis reports the results of a multi year study of the ecology of fish communities in lakes and reservoirs of Labrador, Canada. The work was carried out as part of the Canadian Collaborative Mercury Research Network (COMERN) study of lakes of the boreal forest and undertaken in collaboration with the Innu Nation. The thesis research had two main objectives. The first objective was to evaluate the relevance and implications of a bi-dimensional framework to integrate spatially-explicit energy flows in the definition of consumer feeding ecology and community structure. The second objective was to assess whether spatially-explicit bi-dimensional feeding ecologies and food web structures can improve the assessment of mercury bioaccumulation in fish among boreal aquatic ecosystems. A bi-dimensional framework consists in the integration of horizontal (spatially-explicit) and vertical (trophic) energy flows. In the first half of the thesis, this approach was defined and demonstrated in comparative studies of fish populations and communities from pristine lakes of Labrador. Horizontal energy flows in this case distinguished between littoral and pelagic carbon source contributions to fish consumers in lakes, quantified by variations in stable isotope ratios of carbon in fish tissue. Vertical energy flows described variations in fish trophic position (vertical resource use) quantified by variations in stable isotope ratios of nitrogen in fish tissue.

In the first chapter, the comparative analysis of life-stage and among-lake patterns of vertical trophic position and horizontal reliance on littoral-pelagic carbon in four fish species (Brook Trout, Northern Pike, Long Nose Sucker and White Sucker), demonstrated that bi-dimensional feeding strategies are determined by species ontogeny

and biological and physical ecosystem characteristics. Thus we proposed autecological types to distinguish consumer species having bi-dimensional feeding ecologies shaped mainly by ontogeny (Quis type), by ecosystem features (Ubi type) or both (Aequivocus type). This classification reconsiders the functional role of consumers in two-dimensional space of ecosystems. It also permits the formulation of assumptions regarding consumer flexibility in bi-dimensional resource use in the context of environmental variability (i.e. with greater flexibility in Ubi-type consumers, intermediate flexibility in Aequivocus-type species, and least flexibility in Quis-type consumers). As such, a bi-dimensional approach to consumer feeding ecology may serve to evaluate consumer species sensitivity to disturbance for management or conservations purposes.

In the second chapter, the comparison of lake-specific bi-dimensional food web structures estimated from community averages of fish trophic position and littoral-pelagic foraging, demonstrated that spatially-explicit community organization is related to consumer species composition, to primary productivity constraints at the food web base and to the physical extent of spatially distinct habitats. This indicated that bi-dimensional food web structures provide alternative stable states for consumer communities. We hypothesized that flexibility in bi-dimensional food web structure is related to the sum of consumer species autecological types. Thus at the food web level, a bi-dimensional approach can improve our understanding of the ecological processes that underlie community organization and resilience, and as such facilitate the formulation of appropriate prevention measures and mitigation efforts to limit anthropogenic impacts on natural systems.

In the third chapter, we showed that bi-dimensional resource exploitation by fish integrates spatial influences on Hg exposure and trophic transfers in lake ecosystems. Horizontal reliance on littoral-pelagic carbon source affected fish Hg concentrations. This influence was variable depending on inter-system differences in Hg availability at the base of littoral and pelagic habitats, and inter-specific differences in the type and size of prey consumed across habitat boundaries. Classified by autecological types, bi-dimensional feeding strategies provided species-specific distinctions for the importance of biological and environmental determinants of Hg bioaccumulation in fish, permitting to improve predictions of Hg body burdens by species. Mercury concentrations in Quis-type Northern Pike were highly predictable among lakes using fork length, trophic position and reliance on littoral (versus pelagic) carbon source as positive predictors. This reflected consistent life-history strategies of bi-dimensional resource use and dietary pathways of Hg intake among lake ecosystems in this species. In contrast, mercury concentrations in Ubi-type White Sucker were only faintly explained by age and indirectly related to among-lake differences in growth and littoral-pelagic resource use. This reflected highly variable bi-dimensional dietary pathways of Hg accumulation in this species, as determined by inter-habitat and inter-system differences in prey abundance and resource availability. In Aequivocus-type Long Nose Sucker, the prediction of mercury concentrations was improved by using biological features (fork length and age) with a distinction of community composition and physical ecosystem structure (lake depth) affecting life-stage patterns of littoral-profundal benthic resource use and Hg accumulation. A bi-dimensional framework thus permitted to identify important linkages

between species and ecosystem determinants of Hg bioaccumulation in fish that serve to facilitate the understanding of inter-system variations in fish Hg levels.

In the fourth chapter, a bi-dimensional approach to community structure similarly permitted to identify important linkages between consumer species composition and ecosystem features affecting the extent of Hg bioaccumulation. Horizontal energy flows in this case further distinguished between allochthonous-autochthonous carbon source contributions to primary producer-consumer at the base of food webs. Community-scale and species-specific comparisons confirmed that Hg concentrations in Quis-type consumers like Northern Pike can be used as indicators of inter-system differences in Hg inputs and exposure. The application of a bi-dimensional framework revealed that aquatic ecosystems characterized by greater incorporation of autochthonous-respired carbon at lower trophic levels, by more elaborate consumer communities and longer food chains promoting Hg biomagnification, and by greater reliance on littoral carbon and Hg sources in fish (or greater littoral habitat dimensionality promoting littoral resource use by fish), will reach greater Hg contamination. Together, these factors explained the retention of elevated Hg levels in fish in the Churchill Falls hydroelectric reservoir, more than three decades after impoundment.

Thus wherever spatially distinct carbon sources can be identified and traced through food webs, a bi-dimensional framework provides a solid conceptual basis for spatially-explicit ecological understanding and modeling that facilitates the management of Hg contamination and human exposure across landscapes, and may serve to improve ecosystem, habitat and species conservation and management strategies in the face of

growing anthropogenic perturbations of natural systems and global environmental change.

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APPENDIX 1

METHODOLOGICAL CONSIDERATIONS: STABLE ISOTOPES IN ECOLOGY

The isotopes of an element refer to the different nuclides (or isotope-specific atoms) of this element whose nuclei contains an equivalent number of protons but a different number of neutrons. The addition (or subtraction) of neutral mass does not alter most aspects of chemical reactivity, but is responsible for small discrepancies in the physicochemical properties of elements, known as the isotope effect (Peterson and Fry 1987). Isotope effects (kinetic or equilibrium) cause isotopic fractionation, or the differential partitioning of isotopes between substances (Hoefs 1987). The relative distribution of any two stable isotopes of an element between two different compounds (A and B) (or between different phases of a compound) is measured as the ratio of the heavier to the lighter isotope of this element (R) in each compound (R_A and R_B), and termed fractionation factor α (Hoefs 1987):

$$\alpha_{A\text{-}B}=R_A/R_B$$

Variations in stable isotope ratios are determined by comparing the isotopic composition of a compound to that of a standard reference material, and expressed as delta notation (δ), or parts per thousand (permil (‰)) deviations from the standard (Peterson and Fry 1987):

$$\delta_A\ (‰) =(R_A/R_{standard}-1)*10^3$$

As an example, the carbon isotopic signature of a fish sample corresponds to the ratio of the heavier carbon isotope (^{13}C) to the lighter carbon isotope (^{12}C) in fish tissue, relative

to the same ratio measured in Vienna Pee Dee Belemnite limestone (VPDB), which is the international standard for carbon isotopes:

$$\delta^{13}C_{fish}\ (‰) = [((^{13}C/^{12}C)_{fish} / (^{13}C/^{12}C)_{VPDB}) - 1] * 10^3$$

Positive $\delta^{13}C_{fish}$ values indicate an enrichment in the heavier ^{13}C in fish tissue relative to the standard, while negative values indicate ^{13}C depletion.

Stable isotopes can record two types of information. First, the isotopic distribution of an element in a particular compound may preserve information relative to the origin of this compound. Second, where physical and chemical reactions causing changes in the isotopic distribution of an element are known, observed isotopic compositions may reflect the overall conditions (reactions and/or processes) to which a particular compound was submitted (Peterson and Fry 1987). Stable isotopes are thus excellent environmental tracers, that is, easily detectable substances that behave exactly like the traced material – whilst having at least one distinctive property - that permits to description of variations in the traced material without disturbing or modifying the overall characteristics of the system (Kendall and McDonnel 1998).

Isotopic compositions change in predictable ways as elements cycle in the biosphere, making stable isotope distribution ideally suited to study elements cycles in the environment, through ecosystems, and food webs (Peterson and Fry 1987, Vander Zanden and Rasmussen 2001). Carbon and nitrogen are biologically important elements in food web studies. Biological processes are the most important causes of variations in the isotopic composition of these elements (White 2007). In ecological studies, changes in

stable isotopic composition between a consumer and its food source, from prey to predator, or between any two trophic levels, is measured as trophic fractionation (Δ):

$$\Delta^{13}C_{Prey\text{-}Predator}\ (‰) = \delta^{13}C_{Prey} - \delta^{13}C_{Predator}$$

Carbon is the ultimate source of energy for food webs. Largest fractionation of carbon isotopes occurs during the initial production of organic matter by primary producers. Together, the origin of inorganic carbon sources, different photosynthetic pathways, and carbon availability for uptake by primary producers, yield distinctive carbon isotopic signatures at the food web base (Fry and Sherr 1984, Peterson and Fry 1987, France 1995a). Carbon undergoes little (<1‰) further trophic fractionation in ecological communities, so that carbon isotopic signatures in consumers reflect the relative contributions of distinct carbon sources-fluxes to consumer production (Fry and Sherr 1984). Nitrogen is an essential nutrient for primary productivity, and a fundamental component of all amino acids and proteins. As for carbon, abundance and origin of nitrogen sources determine the extent of nitrogen isotope fractionation by primary producers (Peterson and Fry 1987). Subsequent trophic transfers involve a relatively constant enrichment in the heavier ^{15}N relative to the lighter ^{14}N (of approximately +3‰) between consumers and their food source (DeNiro and Epstein 1981, Minagawa and Wada 1984, Post 2002a). This stepwise enrichment makes nitrogen isotope ratios excellent indicators of trophic positions (Vander Zanden and Rasmussen 1999, Post 2002a).

Inter-system assessments of energy flows and feeding interactions using stable isotope techniques must necessarily take into account both spatial and temporal variability in

carbon and nitrogen pools and stable isotopic values of primary producers at the base of food webs (Vander Zanden and Rasmussen 1999, Post 2002a). This is usually done using system-specific baseline organisms and isotopic signatures for the estimation of carbon pathways and trophic positions in consumers, and the estimation of system-specific food chain length (Vander Zanden and Rasmussen 1999, Vander Zanden and Rasmussen 2001, Post 2002a). Substantial intra- and inter-specific variations in carbon and nitrogen isotopic fractionation between consumers can also conceal subtle differences about the trophodynamics of consumer species and entire food webs. Such variability is related to tissue type and corresponding differences in diet-tissue fractionation (Gannes et al. 1997, Pinnegar and Polunin 1999, McCutchan et al. 2003), to individual metabolic rates and dietary assimilation efficiencies (Gannes et al. 1997, Gaye-Siessegger et al. 2004), to organismal lipid content (for carbon isotopes) (Gannes et al. 1997, Pinnegar and Polunin 1999, McCutchan et al. 2003), and to dietary protein intake and protein quality (for nitrogen isotopes) (Gannes et al. 1997, Pinnegar and Polunin 1999, McCutchan et al. 2003, Robbins et al. 2005, Mill et al. 2007). Mobilization, reorganization and catabolism of stored lipids and proteins during periods of starvation or cessation of feeding (e.g. during reproduction), have also been linked to individual variations (mainly enrichment) in the carbon and nitrogen isotopic compositions of consumers (Doucett et al. 1999, Gannes et al. 1997, McCutchan et al. 2003).

Dietary and food web inferences made from stable isotope ratios of carbon and nitrogen therefore need to take into account inherent differences in carbon and nitrogen pools and fractionation variability between the top and bottom of food webs, and must be made on

the basis of clearly outlined assumptions. Used in concert as carbon source-flux tracers and trophic indicators in comparative rather than absolute studies, isotope ratios of carbon and nitrogen provide an excellent tool to define and compare patterns of consumer resource utilization and ecosystem-specific food web structures.